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LABOULBENIALES ON SEMIAQUATIC HEMIPTERA.
V. *TRICEROMYCES*: WITH A DESCRIPTION OF
MONOECIOUS-DIOECIOUS DIMORPHISM IN THE GENUS

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ABSTRACT

Six species of *Triceromyces* (Laboulbeniales), including the type, *T. balazucii* (on Hebridae), parasitic on semiaquatic Hemiptera, were studied at the light-microscopic level. Descriptions are provided for all of the taxa, and features of developmental morphology are described, compared, and illustrated with photographs and line drawings. Four species are described as new: *T. hebri* (on Hebridae), *T. hydrometrae* (on Hydrometridae), and *T. biformis* and *T. bullatus* (on Mesoveliidae). The species growing on Hebridae and Hydrometridae are monoecious. The two species on Mesoveliidae develop monoecious and dioecious morphs, which occur together on the same host individual. This phenomenon is recognized and described for the first time in the Laboulbeniales. Two species, *Autophagomyces poissonii* and *Dioicomyces mesoveliae*, previously described from a species of Mesoveliidae, are shown to represent the monoecious and dioecious forms of a species of *Triceromyces* and are transferred to this genus as *T. poissonii*. Speculations on the origin of dioecism in the Laboulbeniales are reviewed and discussed briefly without, in the absence of experimental evidence, reaching positive conclusions.

Key words: dimorphism, dioecious, Hemiptera, insects, Laboulbeniales, monoecious, morphology, taxonomy, *Triceromyces*.

INTRODUCTION

The genus *Triceromyces* was established (Majewski 1981) for a species of Laboulbeniales, *T. balazucii* Majewski, characterized by a simple, three-celled receptacle supporting distally on one side a small, several-celled, determinate appendage bearing simple antheridial phialides and on the other side a stalked peritheciium forming three distinctive cellular outgrowths. Characteristics of the genus place it in Tavares's subtribe Stigmatomycetinae of the Laboulbeniaceae (Tavares 1985). The host of *T. balazucii* was one of the velvet water bugs, *Hebrus ruficeps* (Thoms.) (Hemiptera: Hebridae).

Bugs and their relatives have for many years been included in either one order, Hemiptera, classified on the basis of wing structure and the origin of the mouth parts, in two suborders, Homoptera (cicadas, leaf hoppers, aphids, scale insects) and Heteroptera (bugs) (Brues, Melander, and Carpenter 1954; Ross 1965), or in two orders, Homoptera and Hemiptera (=Heteroptera) (Comstock 1947; Borror, DeLong, and Triplehorn 1981; Arnett 1985). I earlier adopted the latter concept in my studies of Laboulbeniales on semiaquatic Hemiptera (Benjamin 1979). Hemiptera serve as hosts for a number of Laboulbeniales, but Homoptera still are without known laboulbenialean parasites.

There is now a trend away from the traditional classification of Hemiptera (i.e., Heteroptera) into the long-horned bugs¹ or Gymnocerata, often divided into two groups Amphibicorizae (aquatic or shore inhabiting) and Geocorizae (terrestrial), and the short-horned bugs or Cryptocerata also called Hydrocorizae (aquatic and semiaquatic) (Comstock 1947; Borror et al. 1981). Instead, these insects are dis-

tributed into seven infraordinal taxa (Štys and Kerzhner 1975) by some entomologists (Menke 1979; Polhemus 1985) with the Hydrocorizae being included in one infraorder, Nepomorpha, the Amphibicorizae in two infraorders, Gerromorpha and Leptopodomorpha, and the Geocorizae in four infraorders, Cimicomorpha, Dipsocoromorpha, Eniocephalomorpha, and Pentatomomorpha. Members of four of these infraorders are known to harbor Laboulbeniales: Cimicomorpha, Gerromorpha, Nepomorpha, and Pentatomomorpha.

Only a few Laboulbeniales are known to parasitize Hemiptera, but additions made during the past 20 years have brought the number of recognized taxa to 51 species and one variety. Early contributions were by Thaxter who described three genera with species known only on Hemiptera: *Coreomyces* (15 spp.) on Corixidae (Nepomorpha) (Thaxter 1902, 1905, 1918, 1931); *Polyandromyces* (1 sp., 1 var.) on Pentatomidae (Pentatomomorpha) (Thaxter 1920); and *Rhizopodomyces* (1 sp.) on Hebridae (Gerromorpha) (Thaxter 1931). Thaxter also described two species of *Laboulbenia* Mont. & Robin on Veliidae (Gerromorpha) (Thaxter 1912) and single species of *Stigmatomyces* Karsten (later transferred to *Hesperomyces* Thaxt. [Thaxter 1931] and then to *Acompsomyces* Thaxt. [Tavares 1985]) on Anthocoridae (Cimicomorpha) (Thaxter 1917), *Corethromyces* Thaxt. on Lygaeidae (Pentatomomorpha) (Thaxter 1931), and *Autophagomyces* Thaxt. on Veliidae (Thaxter 1931). Five species were added to *Coreomyces*, four by Spegazzini (1917, 1918) and one by Poisson (1929, as *Paracoreomyces* Poisson). Very recently a monotypic new genus, *Majewskia*, resembling *Kainomyces* Thaxt., has been described by Lee and Sugiyama (1986) from a species of Cydnidae (Pentatomomorpha). All other Laboulbeniales described from Hemiptera have been found on Gerromorpha. Eight species of *Laboulbenia* on Veliidae (6 spp.) and Macroveliidae (2 spp.) were described by Benjamin (1967) who also added six species of *Rhizopodomyces* on Hebridae (Benjamin 1979). *Prolixandromyces*, with two species on Veliidae, was described by Benjamin (1970) and subsequently augmented by three species on members of the same family (Benjamin 1981). Finally, Majewski (1981) described two genera on Hebridae, *Tavaresiella*, with one species, and *Triceromyces*, the subject of this paper.

To the above listing must be added two taxa on Mesoveliidae (Gerromorpha) characterized by me some years ago (Benjamin 1970), *Autophagomyces poissonii* Benjamin and *Dioicomyces mesoveliae* Benjamin. Although both species share certain characteristics in common, especially the nature of the receptacle and perithecium, they differ in that one, *A. poissonii*, is monoecious whereas the other, *D. mesoveliae*, is dioecious. When I originally studied these taxa, assignment of the monoecious form to *Autophagomyces*, despite some differences in receptacular structure, was made primarily on the basis of the *Autophagomyces*-like appendage and the known occurrence of a species of *Autophagomyces* on a member of a related family, the Veliidae (Benjamin 1967; Thaxter 1931). Except for its *Dioicomyces*-like male, the dioecious form did not in several ways fit the concept of *Dioicomyces* Thaxter (Thaxter 1908, 1931), for not only was there a marked difference between the structure of the receptacle of *D. mesoveliae* and that of other species of *Dioicomyces* but also the appendage—always one celled in species of *Dioicomyces*—was two celled in *D. mesoveliae*. However, there being no precedent for doing otherwise, I assigned the monoecious form to *Autophagomyces*, where it appeared logically to fit, and, for the same reason, I forced the dioecious form into *Dioicomyces*.

Since 1970, I have had an opportunity to study many additional Laboulbeniales occurring on semiaquatic Hemiptera. Some of these, as mentioned above, have been described (Benjamin 1979, 1981). Others remain to be dealt with. Included with the latter are four taxa assignable to *Triceromyces*. Two of these, which grow on Mesoveliidae, exist unquestionably as coexisting monoecious and dioecious forms of single species. This discovery points to a need for reevaluating the taxonomic status of *A. poissonii* and *D. mesoveliae*, which must be regarded as belonging to one and the same species of *Triceromyces*. The purpose of this paper is to emend the generic concept of *Triceromyces*, to describe four additional species of the genus, to change the generic status of *A. poissonii* and *D. mesoveliae*, and report for the first time the existence of monoecious-dioecious dimorphism in the Laboulbeniales.

MATERIALS AND METHODS

All of the fungi examined in this study were taken from insects stored for more or less extended periods of time in 50–75% ethyl alcohol. Collection data for all of the hosts are given following the descriptions.

Fungi were mounted in glycerine containing a trace of cotton blue or acid fuchsin. Prior to mid-1979, I employed a mounting technique essentially like that used by Thaxter (1896) in which the fungi were mounted under a single cover glass, which was sealed to the slide by a shellac-based ringing compound (Benjamin 1971). Subsequently, I have adopted a modification of this technique in which specimens are mounted between two cover glasses.

The procedure for preparing slide mounts is the same as that given earlier (Benjamin 1971) up to step *e*. After removal from the host, fungi are transferred to a minute drop of Hoyer's medium placed in the center of a 22-mm cover glass (square or circle) carried on a slide for easy manipulation under the dissecting microscope. A bit of the Hoyer's medium is moved a short distance from the specimens and a few paper fibers are affixed to help prevent undue distortion of the fungi when the second cover glass is added. A small drop of the glycerine-dye mixture is placed in the center of an 18-mm cover glass (square or circle), which is carefully inverted over the specimens on the larger cover glass. Care should be taken to assure precise centering of the smaller glass on the larger. Practice is needed in applying an amount of glycerine (it isn't much!) sufficient only to fill the space between the two cover glasses. The mounting medium is best dispensed with a squeeze-type plastic dropper bottle having a tiny orifice (the kind used for administering eye drops is excellent). A small drop of pure glycerine now is applied to the center of the small cover glass of the two-cover glass combination and the preparation is inverted and placed on a glass microscope slide. Positioning of the cover glasses on the slide depends on one's personal preference for attaching the label or labels. Again, with practice one can dispense a drop of glycerine just sufficient to flow to the edge of the small cover glass. Allow time for the glycerine to reach the edge before proceeding to the next step. The glycerine seal helps prevent formation of flattened air bubbles under the preparation due to uneven inwelling of the sealing compound. Finally, the large cover glass, now uppermost, is sealed to the slide by the addition—at opposite sides and in excess of the amount needed to fill the space under the large cover glass—of a medium like Balsam, which hardens in time. I use COVERBOND[®] (Harleco, Gibsonville, New Jersey 08027). Slides are immediately placed on a slide warmer set at ca. 45 C. Several

slightly flattened lead shot are placed on the cover glass to hold the preparation securely in place while the sealing material hardens around the edges of the larger cover glass. This small amount of weight does not affect the specimens and it assures a flat mount. In 24–48 h the now-hardened excess sealing compound extending beyond the edge of the cover glass is carefully removed by means of a razor blade. I usually return the slide to the slide warmer for an additional 2–3 days for further hardening of the sealing compound. Slides should be stored flat.

The above technique enables one to mount specimens in a liquid medium, like glycerine, and have slides with a degree of permanence not obtainable with ordinary ringed mounts.

A Leitz Dialux microscope equipped with differential interference contrast optics was used for making all microscopic observations and taking photographs. The same instrument, equipped with a camera lucida, was employed for preparing drawings. Photographs were taken on 4 in. × 4 in. Kodak Technical Pan Film #2415 and developed in Kodak HC-110 diluted to give an ASA value of 100.

Terminology and abbreviations used to describe thalloid structures discussed in the text and depicted in the figures are, with a few exceptions, those of Tavares (1985:431–434).

TAXONOMY

TRICEROMYCES Majewski, Acta Mycol. 16:149, (1980)1981, emended R. K. Benjamin.

Receptacle of a monoecious form or a female form consisting of three cells; the basal cell (I) small, subtending the relatively elongate subbasal cell (II) and terminal cell (III), which are laterally adnate and more or less parallel to one another. Cell III secondarily divided into an upper, nucleate cell and a lower, empty segment. Primary appendage, subtended by cell III, free; in a monoecious form consisting of a stalk composed of three superposed sterile cells subtending two or more superposed fertile cells, each of which gives rise, internally, to usually one simple antheridium, rarely terminated by a sterile prolongation; in a female form consisting of two, rarely three, superposed sterile cells. Perithecium, subtended by cell II, with well-defined stalk and basal cells, four vertical rows of outer wall cells of four or five cells each, and a single ascogenic cell; with or without one or more prominent outgrowths from outer wall cells below the apex. Male forms consisting of three superposed cells terminated by single simple antheridia.

Type species: Triceromyces balazucii Majewski.

Majewski's (1981) description of *Triceromyces* indicated only four cells in each vertical row of outer wall cells. In my study of six species of the genus, including the type, I definitely found five cells in some of the rows. Despite much effort, using the fungus material and optics at hand, I could not satisfy myself that this is true of all the rows.

A KEY TO THE SPECIES OF *TRICEROMYCES*

- A. Perithecia with one or more prominent outgrowths from outer wall cells; only monoecious individuals known B
- Perithecia lacking such outgrowths from outer wall cells; associated monoecious and dioecious forms known (on Mesoveliidae) D

- B. Appendage giving rise to (4)–5–6(–7) lateral, inwardly directed antheridia (on Hydrometridae) 3. *T. hydrometrae*
 – Appendage giving rise to only three upwardly directed antheridia (on Hebridae) C
 C. Perithecium bearing one short and two elongate outgrowths 1. *T. balazucii*
 – Perithecium bearing only one elongate outgrowth 2. *T. hebri*
 D. Perithecial wall bullate in part 5. *T. bullatus*
 – Perithecial wall smooth E
 E. Primary appendage of female form slender, elongate, 35–51 μm long, 6–9 μm wide at the base 4. *T. biformis*
 – Primary appendage of female form shorter and broader, 26–34 μm long, 9–13 μm wide at base 6. *T. poissonii*

1. TRICEROMYCES BALAZUCII Majewski, Acta Mycol. 16:150, (1980)1981.

Fig. 1–5, 54

Pale yellowish brown; the perithecial apex, the proximal surface of the upper perithecial outgrowths, and the lowermost cell of the antheridiiferous part of the appendage darker.

Receptacle: About two times longer than broad, 48–55 μm by 22–25 μm distally, often somewhat curved near the foot; basal cell small, 13–17 μm long by 9–11 μm wide immediately below cells II and III, which are subequal; cell II 35–38 \times 11–13 μm ; cell III 31–37 \times 12–15 μm , the upper part becoming separated from the lower part by a secondary cross wall, forming an elongate cell, rounded below, 25–30 \times 12–15 μm .

Appendage: The three-celled stalk 33–36 μm long, 11–15 μm wide; the cells subequal; the distal antheridiiferous part consisting of two cells, separated from the upper cell of the stalk by a darkened septum; the basal cell 12–15 μm high, 11–15 μm wide, bearing one upwardly directed antheridium; the upper cell smaller, subtending two nearly erect antheridia; antheridia 17–19 \times 5–7 μm , the venters united, the efferent tubes free. Total length to tip of uppermost antheridium 59–65 μm .

Perithecium: Stalk cell (VI) about twice as long as broad, 20–25 μm long; secondary stalk cell (VII) shorter, triangular in lateral view, 12–17 μm wide; basal cells (*m*, *n*, *n'*) constituting ca. 30% of the total length of the body above the stalk cells; body externally convex, about two times longer than broad including the basal cells, widest near the middle, 130–160 μm long, including the stalk cells, 57–63 μm wide, somewhat curved distally, the apex blunt; the basal cell of the posterolateral row of outer wall cells derived from basal cell *m* forming a broadly rounded protuberance 8–13 μm high by 22–30 μm wide at the base; the next cell above in the same row forming an elongate, divergent outgrowth, 73–85 μm long, 20–23 μm wide at the base, 10–17 μm wide at its narrowest, where it bends outward and forms a foot-shaped projection 30–40 μm long by 16–20 μm wide at the base, the whole outgrowth resembling a human lower leg and foot as viewed laterally; the subterminal cell of the *m* row of outer wall cells bearing, near its base, the broad, circular, darkened trichogynic remnant 7–10 μm in diameter; the small terminal cell of the *m* row broadly truncate and darkened apically; the fourth cell of the outer row of wall cells derived from basal cell *n'* giving rise distally to an elongate, curved, apically rounded outgrowth, 40–47 μm long, which is separated by a proximal cross wall into a lower cell, 10–15 \times 18–20 μm , and

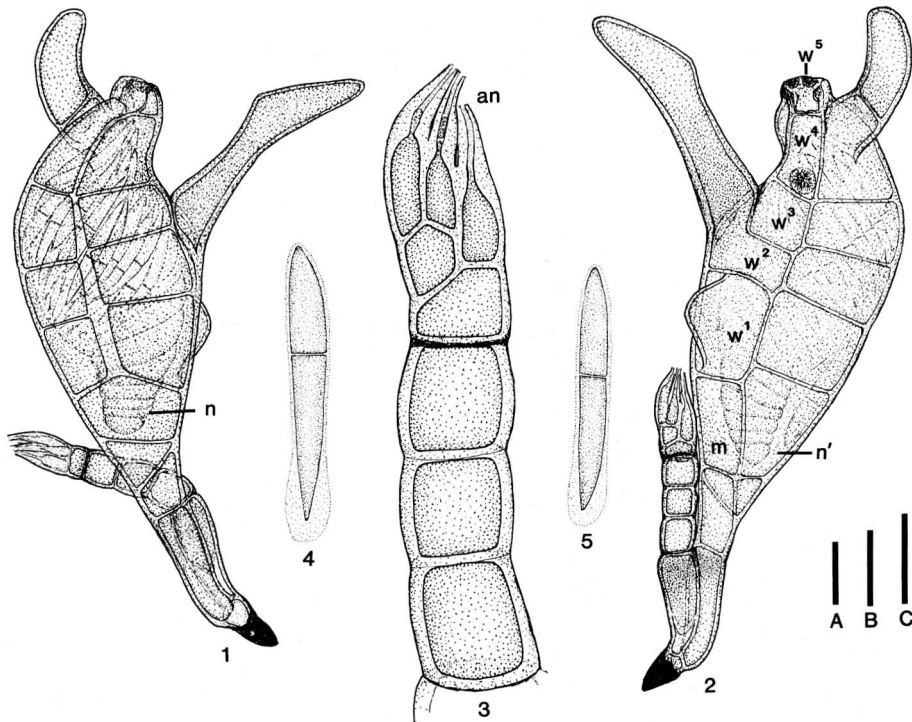


Fig. 1-5. *Triceromyces balazucii* (Majewski 1584).—1-2. Two mature individuals viewed from opposite sides.—1. Because the specimen was somewhat compressed in the slide mount, the three proximal cells of the two vertical rows of outer wall cells derived from basal cell *n* were slightly separated.—2. This specimen shows the relationship of the three perithecial outgrowths to the outer wall cells of the two rows of wall cells derived from basal cells *m* and *n'*. The outer wall cells are designated *w*¹ to *w*⁵ from base to tip. Note the large trichogynic remnant near the base of the subterminal outer wall cell (*w*⁴) of the *m* row.—3. Mature appendage showing the three-celled stalk and the distal antheridiiferous part. Note the relationship of the three basally adnate antheridia to the two subtending cells.—4-5. Ascospores. (Fig. 1-2, bar A = 20 μ m; Fig. 3, bar C = 10 μ m; Fig. 4-5, bar B = 10 μ m.)

an upper cell, 30–35 \times 15–18 μ m; cells of the two rows of outer wall cells derived from basal cell *n* unmodified, each row consisting of four (?five) cells. Ascospores hyaline, 33–40 \times 5 μ m (less sheath).

Total length from tip of foot to tip of perithecium 190–210 μ m.

Specimens examined.—POLAND: Długie near Izbica Kujawska (Włocławek voivodeship), 22 May 1976, T. Majewski coll. (No. 1584), on the legs of *Hebrus ruficeps* Thoms. (Hemiptera: Hebridae).

My description of *T. balazucii* is based on nine mature individuals in good condition on a slide mount prepared by Dr. Majewski that was sent to Dr. Isabelle Tavares who kindly lent it to me for study. I had received from Dr. Majewski, in Aug. 1981, two slides bearing two immature and two mature specimens of the species, which were more or less compressed and broken and in rather poor condition for critical study. My measurements of the species differ slightly from those given by Majewski, who examined some 20 specimens in preparing his description. The receptacle and appendage of *T. balazucii* and *T. hebri* are very

similar, but the two species are readily distinguished by the conformation of their perithecial apices and in the number and nature of their perithecial outgrowths.

2. *Triceromyces hebri* Benjamin, sp. nov.

Fig. 6–13, 55

Thallus dilutus flavus; superficies partis superi cellulae III receptaculii cum brunnea tincta; superficies cellulae infimae partis antheridiiferi cum brunnea tincta. *Receptaculum* plerumque valde curvatum 47–53 μm altum 22–26 μm in maxima latitudine. Cellula I parva 18–20 \times 10 μm . Cellula II 30–35 \times 10–12 μm . Cellula III 25–27 \times 12–16 μm ; pars superum cellulae cellulam 12–25 \times 12–16 μm formans. *Appendix* 78–84 μm longa. Stipes 40–48 μm longum; septum superum fuscum; cellula basilaris 16–20 μm alta 17–20 μm lata; cellula media brevior 14–16 \times 15–20 μm ; cellula terminalia brevissima 10–15 \times 14–18 μm . Pars antheridiiferum bicellulare; cellula infima 10–13 μm alta 14–18 μm lata antheridium singulum erectum gignens; cellula supra brevior antheridia duo erecta gignens. Antheridia 20–25 \times 5–6 μm ; venteres antheridiorum basi conjuncti. *Perithecium* fere symmetricum, marginibus prope uniformiter convexis, 130–162 μm longum (cum stipite et cellulis basilaribus) 35–56 μm latum. Cellulae basillares (*m*, *n*, *n'*) prope 0.3 corporis perithecii in tota longitudine. Cellula VI 22–29 \times 10–13 μm . Cellula VII a latere visa triangularis 20–25 \times 10–12 μm . Cellula basilaris seriei cellulosa ex *m*-cellula basilari oriunda prominentiam elongatum 50–75 \times 13–18 μm faciens. Ascosporae hyalinae 40–45 \times 6 μm (sine vagina). Thallus totus 165–195 μm longus ad apicem perithecii. Typus RKB 2702 (RSA).

Pale yellow; the surface of the upper part of cell III of the receptacle and lowermost cell of the antheridiiferous part suffused with brown.

Receptacle: About two times longer than broad, 47–53 μm long by 22–26 μm wide distally, often abruptly curved near the middle; basal cell small, 18–20 μm long by 10 μm wide immediately below cells II and III, which are subequal; cell II 30–35 \times 10–12 μm ; cell III 25–27 \times 12–16 μm , the upper part becoming separated from the lower part by a secondary cross wall, forming a basally rounded cell 12–15 \times 12–16 μm .

Appendage: The three-celled stalk 40–48 μm long; the basal cell slightly rounded externally, 16–20 μm long, 17–21 μm wide; the next two cells above subequal, median cell 14–16 \times 15–20 μm , upper cell 10–15 \times 14–18 μm ; the distal antheridiiferous part consisting of two cells, separated from the upper cell of the stalk by a darkened septum; the basal cell 10–13 μm high, 14–18 μm wide, bearing one upwardly directed antheridium; the upper cell smaller, subtending two nearly erect antheridia; antheridia 20–25 \times 5–6 μm , the venters united, the efferent tubes free. Total length to tip of uppermost antheridium 78–84 μm .

Perithecium: Stalk cell (VI) elongate, 22–29 \times 10–13 μm , often once transversely plicate on the outer side immediately below the secondary stalk cell (VII), which is more or less triangular in lateral view, 20–25 \times 10–12 μm ; basal cells (*m*, *n*, *n'*) constituting ca. 30% of the total length of the body above the stalk cells; body externally convex, 130–162 μm long including the stalk and basal cells, 35–56 μm wide, the apex broadly rounded, curved inward slightly; the basal cell of the posterolateral row of outer wall cells derived from basal cell *m* forming an elongate, divergent, apically rounded outgrowth 50–75 \times 13–18 μm , which is basally adnate to the outer wall of the perithecium up to about the middle of the third tier of wall cells; the subterminal cell of the *m* row of outer wall cells bearing, near its base, the broad, circular trichogynic remnant 8–10 μm in diameter; the tip of the small terminal cell of the *m* row forming a small, rounded prominence; the anterolateral row of outer wall cells derived from basal cell *n'* consisting of

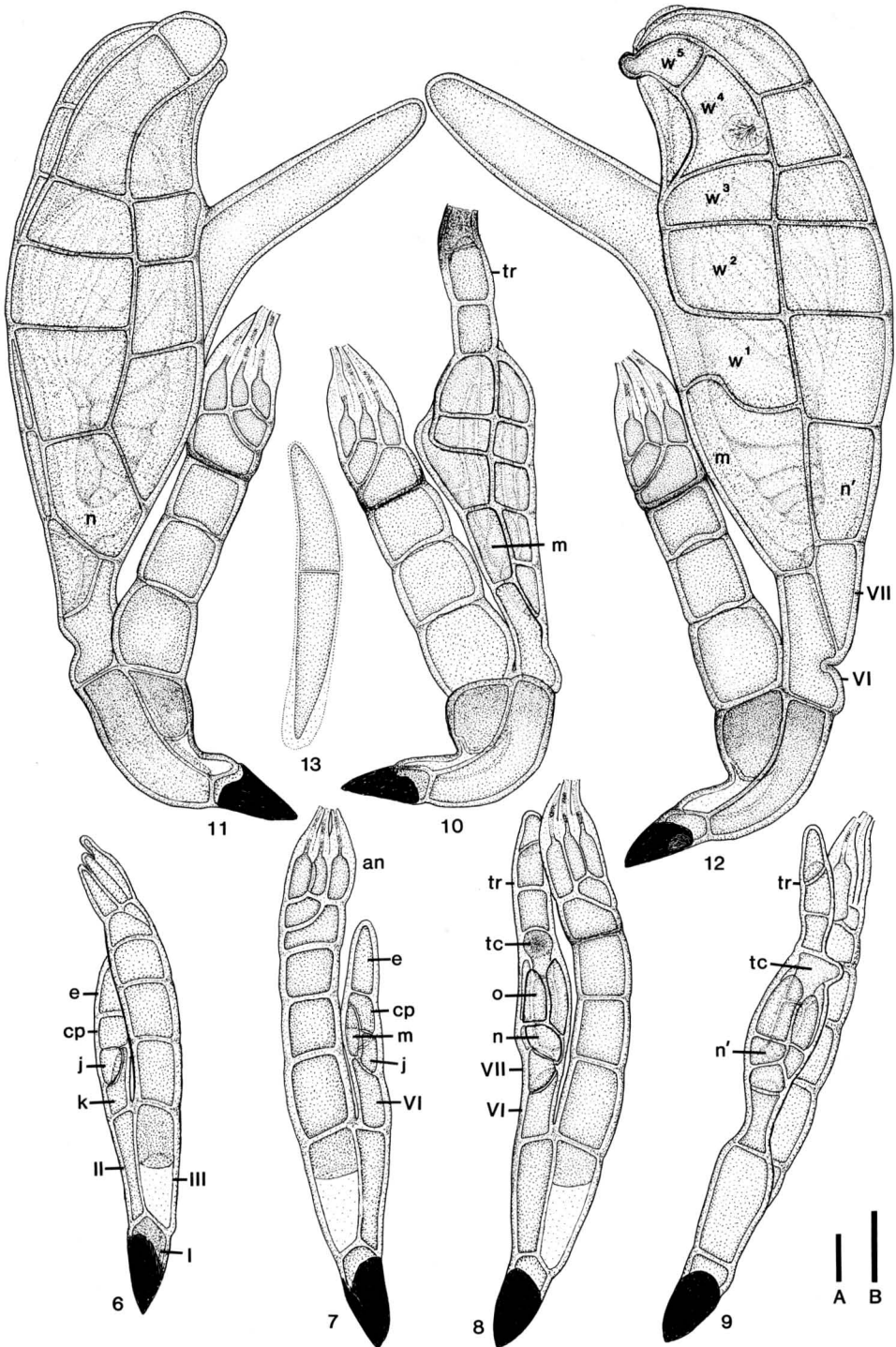


Fig. 6-13. *Triceromyces hebri* (RKB 2702).—6-10. Early stages of development of the thallus. Details and terminology are given in the text. Figures 8 and 9 represent two views of the same individual (the second drawing was made following a shift of the specimen in the mount). In Fig. 10, note the

five cells, the terminal cell nearly two times longer than the subterminal; the anterolateral row of outer wall cells derived from basal cell *n* consisting of five cells, the terminal cell nearly three times shorter than the subterminal cell; the posterolateral row of outer wall cells derived from basal cell *n* consisting of four (?five) cells. Ascospores $40\text{--}45 \times 6 \mu\text{m}$ (less sheath).

Total length from tip of foot to tip of peritheciium 165–195 μm .

Etymology.—Named for the host genus, *Hebrus*.

Holotype.—MEXICO: Jalisco: Ixcatlan, 24 Nov. 1968, J. T. Polhemus coll. (CL 1225). On the lower left side of the abdomen of *Hebrus* sp. (Hemiptera: Hebridae); RKB 2702 (Fig. 12); slide in RSA.

The description is based on 10 mature adults found on only one of four specimens of the host received from Dr. Polhemus. Despite the excellent condition of the material, I could not determine for sure if the posterolateral row of outer wall cells derived from basal cell *n* consists of five or four cells. The position of the cross walls separating the five adjacent cells in the other rows is easily determined. Characteristics distinguishing this species from *T. balazucii*, which it resembles, already have been mentioned above following the description of the latter.

3. *Triceromyces hydrometrae* Benjamin, sp. nov.

Fig. 14–31, 56, 81–82

Thallus dilutus flavus; superficies postica receptaculi et appendicis ex brunnea flava. *Receptaculum* paene rectum $50\text{--}60 \mu\text{m}$ altum $17\text{--}20 \mu\text{m}$ in maxima latitudine. Cellula I $20\text{--}28 \times 6\text{--}8 \mu\text{m}$. Cellula II $27\text{--}31 \times 8\text{--}10 \mu\text{m}$. Cellula III $29\text{--}35 \times 10\text{--}12 \mu\text{m}$; pars superum cellulae cellulam $21\text{--}27 \times 10\text{--}12 \mu\text{m}$ formans. *Appendix* $100\text{--}127 \mu\text{m}$ longa. Stipes $48\text{--}57 \times 11\text{--}13 \mu\text{m}$; cellulae subaequales paene cylindricae; septum superum fuscum. Pars antheridiiferum ex (4–)5–6(–7) cellulis constans; antheridium singulum in quoque cellula formatum; cellula terminalis prolongationem elongatum gracile productens; cellula basilaris plerumque spinam parvum inconspicuum ferens. Antheridia paene liberum $27\text{--}37 \times 5\text{--}7 \mu\text{m}$. *Peritheciium* elongatum relative gracile plus minusve convexum $190\text{--}260 \mu\text{m}$ longum (cum stipite et cellulis basilaribus) $32\text{--}50 \mu\text{m}$ latum; pars terminale basi constrictum collum gracile curvatum $52\text{--}60 \times 14\text{--}20 \mu\text{m}$ faciens; apex obtusum processibus duo curtis posticis $8\text{--}12 \times 7\text{--}10 \mu\text{m}$. Cellulae basillares (*n*, *n'*, *m*) prope 0.2 corporis perithecii in tota longitudine. Cellula VI tenuis elongata $25\text{--}35 \times 12\text{--}15 \mu\text{m}$. Cellula VII relative parva perangusta $15\text{--}18 \mu\text{m}$ longa. Cellula subterminalis seriei cellulosa ex *m*-cellula basilari oriunda prominentiam curta rotundata $10\text{--}20 \times 7\text{--}12 \mu\text{m}$ faciens. Ascospores hyalinae $40\text{--}45 \times 5\text{--}6 \mu\text{m}$ (sine vagina). Thallus totus $230\text{--}300 \mu\text{m}$ longus ad apicem perithecii. Typus RKB 2891 (RSA).

Pale yellow to nearly hyaline; the posterior surface of the receptacle and appendage tinged with brown.

Receptacle: About three times higher than wide, $50\text{--}60 \mu\text{m}$ high by $17\text{--}20 \mu\text{m}$ wide distally, nearly straight; basal cell slender, $20\text{--}28 \mu\text{m}$ long by $6\text{--}8 \mu\text{m}$ wide

←

beginning stage of development of the perithecial upgrowth from the basal cell of the row of outer wall cells derived from basal cell *m*.—11–12. Two mature individuals viewed from opposite sides. Figure 11 shows the two vertical rows of outer wall cells derived from basal cell *n*. Figure 12 shows the single rows of outer wall cells derived from basal cells *m* and *n'*. Note the relationship of the perithecial outgrowth, derived from the basal cell (*w*¹) of the *m* row, and the trichogynic remnant near the base of the subterminal cell (*w*²) of the same row.—13. Ascospore. (Fig. 6–12, bar A = $10 \mu\text{m}$; Fig. 13, bar B = $10 \mu\text{m}$.)

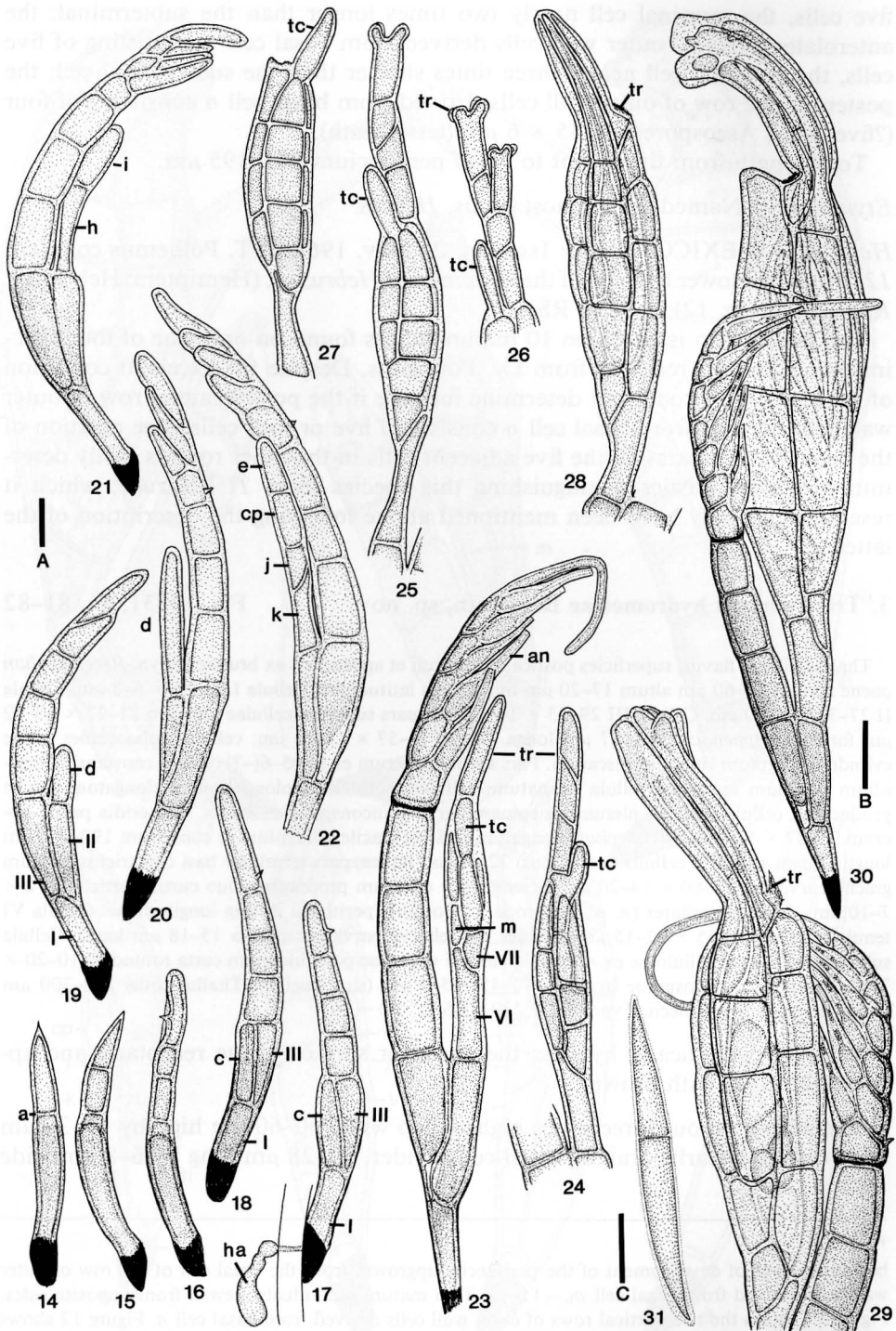


Fig. 14–31. *Tricoromyces hydrometrae* (RKB 2890, 2891, 2892).—14–29. Stages of development of the receptacle, appendage, and perithecium. Details and terminology are given in the text. The young individual shown in Fig. 17 was growing on an antenna of the host and shows a small saccate

immediately below cells II and III, which are subequal; cell II, $27-31 \times 8-10 \mu\text{m}$; cell III, $29-35 \times 10-12 \mu\text{m}$, the upper part becoming separated from the lower part by a secondary cross wall, forming an elongate cell $21-27 \times 10-12 \mu\text{m}$.

Appendage: The three-celled stalk $48-57 \times 11-13 \mu\text{m}$; the cells subequal, nearly cylindrical; the distal antheridiiferous part consisting of (4-)5-6(-7) cells, separated from the upper cell of the stalk by a darkened septum; each cell bearing a single, inwardly and upwardly directed, nearly free antheridium; the terminal cell forming an elongate, slender prolongation $25-80 \times 3-4 \mu\text{m}$; the basal cell often bearing, on its outer margin, a small, inconspicuous spinose projection; antheridia $27-37 \times 5-7 \mu\text{m}$. Total length to tip of uppermost antheridium $100-127 \mu\text{m}$.

Perithecium: Stalk cell (VI) slender, elongate, $25-35 \times 12-15 \mu\text{m}$; secondary stalk cell (VII) relatively small, longer than broad as viewed laterally, $15-18 \mu\text{m}$ long; basal cells (*m*, *n*, *n'*) constituting ca. 20% of the total length of the body above the stalk cells; body elongate, relatively slender, externally slightly convex, broadest near the middle, $190-260 \mu\text{m}$ long, including the stalk and basal cells, by $32-50 \mu\text{m}$ wide; the terminal part constricted at the level of the trichogynic remnant and forming a slightly curved neck $52-60 \times 14-20 \mu\text{m}$; the apex blunt, with two short, rounded outgrowths $8-12 \times 7-10 \mu\text{m}$, derived from the short upper cells of the posterolateral rows of outer wall cells derived from basal cells *m* and *n*; the third cell of the posterolateral row of outer wall cells derived from basal cell *m* growing upward and forming a bluntly rounded projection $10-20 \mu\text{m}$ long by $7-12 \mu\text{m}$ wide at the base; the trichogynic remnant, near the base of the fourth cell of the *m* row, $5-7 \mu\text{m}$ wide; the anterolateral rows of outer wall cells derived from basal cells *n'* and *n* consisting of four (?five) cells. Ascospores $40-45 \times 5-6 \mu\text{m}$ (less sheath).

Total length from tip of foot to tip of perithecium $230-300 \mu\text{m}$.

Etymology.—Named for the host genus, *Hydrometra*.

Holotype.—U.S.A.: Arizona; Pima Co.; Santa Catalina Mts., Sabino Canyon, 10 Oct. 1959, F. S. Truxal and L. M. Martin coll. On legs and antennae of *Hydrometra martini* Kirkaldy (Hemiptera: Hydrometridae); *RKB 2891* (one δ); slides in RSA.

Other specimens examined.—Collection data and host as for the holotype. On legs and antennae of *RKB 2890* (one φ) and *RKB 2892* (one δ); slides in RSA.

This is the first record of Laboulbeniales on a member of the Hydrometridae, and the three specimens of the host cited above provided excellent material for study—47 mature and 68 immature individuals, and 24 broken adults lacking perithecia. Aspects of development of the species will be discussed in the next section of this paper. *Triceromyces hydrometrae* can be distinguished from other members of the genus in several ways, as can be seen from the illustrations. Especially prominent are the elongate, multicellular fertile part of the appendage with its variable number of antheridia and terminal sterile prolongation, and the narrow, basally constricted, subapically bilobate perithecial neck.

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haustorium (*ha*) developed in the antennal lumen following penetration of the thick cuticle.—30. A mature individual.—31. Ascospore. (Fig. 14–29, bar A = $10 \mu\text{m}$; Fig. 30, bar B = $20 \mu\text{m}$; Fig. 31, bar C = $10 \mu\text{m}$.)

4. *Triceromyces biformis* Benjamin, sp. nov.

Fig. 32–53, 57–58

Forma Monoeca

Thallus dilute flavus; superficies posticae receptaculi et apicis perithecialis brunnea. *Receptaculum* rectum vel parum curvatum 37–45 μm altum. Cellula I 17–20 \times 8–9 μm . Cellula II 18–25 \times 10–12 μm . Cellula III 20–27 \times 8–11 μm ; pars superum cellulam 12–17 \times 8–11 μm formans. *Appendix* 75–120 μm longa. Stipes 35–45 \times 7–9 μm ; septum supernum fuscum. Cellulae basiliares et terminales subaequales ca. 15 μm longae. Cellula media ca. 11 μm longa. Pars antheridiiferum bicellulare; cellula infima elongata 12–20 \times 6–8 μm antheridium singulum erectum cellulae superae a latere adnatum gignens; cellula supra brevior antheridium singulum erectum liberum gignens. Antheridia 21–35 \times 5–7 μm . *Perithecium*: Cellula VI 22–35 \times 14–18 μm . Cellula VII variabilis 17–70 μm longa. Cellula *m* cellulae basilaris 30–70(–95) μm longa. Pars ex cellulis basilaribus *n* et *n'* 17–50 μm longum compositum. Cellulae VI, VII, *m*, *n*, et *n'* stipitem perithecialem 55–120 \times 17–23 μm facientes. Corpus perithecii supra cellulam basiliarem 112–153 \times 42–50 μm plus minusve uniformiter inflatum. Apex perithecii rotundatum plerumque inflexus. Ascosporae hyalinae 45–50 \times 4–5 μm (sine vagina). Thallus totus 200–310 μm longus ad apicem perithecii.

Forma Dioecia

Color feminae idem ac formae monoecae; mas dilutus flavus supra pedem.

Mas.—Cellula basilaris (receptaculum) 24–34 \times 5–8 μm . Cellula media 10–16 \times 5–8 μm . Cellula supra 8–10 \times 5–8 μm . Antheridium 20–29 \times 6–9 μm . Thallus totus 60–88 μm .

Femina.—*Receptaculum* idem ac formae monoecae 35–42 μm longum. Cellula basilaris 15–30 \times 8–9 μm . Cellula II 17–22 \times 8–10 μm . Cellula III 20–25 \times 8–10 μm ; parte superum cellulam 12–17 \times 8–10 μm formans. *Appendix* 37–52 μm longa. Cellula infima 12–18 \times 6–9 μm . Cellula suprema 25–34 \times 6–9 μm raro divisa. *Perithecium* idem ac formae monoecae. Cellula VI 20–31 \times 15–18 μm . Cellula VII 13–21 μm longa. Cellula *m* 31–38 μm longa. Pars ex cellulis basilaribus *n* et *n'* 15–25 μm longum compositum. Cellula VI, VII, *m*, *n*, et *n'* stipitem perithecialem 40–50 \times 17–20 μm facientes. Corpus perithecii supra cellulam basiliarem 110–140 \times 44–50 μm . Ascosporae hyalinae 46–51 \times 5 μm (sine vagina). Thallus totus 200–224 μm longus ad apicem perithecii. Typus *RKB 2846* (RSA).

Monoecious Form

Pale yellow; the posterior surfaces of the receptacle and perithecial apex above the third tier of outer wall cells dark brown.

Receptacle: Straight or slightly curved, 37–45 μm high; basal cell, 17–20 μm long by 8–9 μm wide immediately below cells II and III, which are subequal; cell II, 18–25 \times 10–12 μm ; cell III, 20–27 \times 8–11 μm , the upper part becoming separated from the lower part by a secondary cross wall, forming a basally rounded cell 12–17 \times 8–11 μm .

Appendage: The three-celled stalk 35–45 \times 7–9 μm ; the cells cylindrical; the lower and upper cells subequal, averaging 15 μm long; the median cell shorter, averaging 11 μm long; the distal antheridiiferous part consisting of two cells, separated from the upper cell of the stalk by a slightly darkened septum; the lower cell elongate, 12–20 \times 6–8 μm , subtending an upwardly directed antheridium, which is laterally adnate on the inside to the smaller upper cell; the latter subtending a free antheridium; antheridia 21–35 \times 5–7 μm . Total length to the tip of the upper antheridium 75–120 μm .

Perithecium: Stalk cell (VI) longer than broad, 22–35 \times 14–18 μm ; secondary stalk cell (VII) variable, 17–70 μm in length, as is basal cell *m*, which is 30–70(–

95) μm in length; combined length of cells n and n' 17–50 μm ; the stalk cells and basal cells forming a perithecial stipe of variable length from about 55 μm up to 120 μm and 17–23 μm wide at mid-height; body above the basal cells $112\text{--}153 \times 42\text{--}50 \mu\text{m}$, more or less uniformly inflated, broadest near the middle, the distal one third often bent inward and tapered to the rounded tip, which may be abruptly concave on the outside; the posterolateral row of outer wall cells derived from basal cell m consisting of five cells, the upper two subequal and slightly shorter than the three cells below, the trichogynic remnant, 7–8 μm wide, located near the base of the fourth cell; the three rows of outer wall cells derived from basal cells n' and n consisting of four (?five) cells. Ascospores $45\text{--}50 \times 4\text{--}5 \mu\text{m}$ (less sheath).

Total length from tip of foot to tip of perithecium 200–310 μm .

Dioecious Form

Pigmentation of female as for monoecious form; male pale yellow above the foot.

Male individual.—Basal cell (receptacle) including foot $24\text{--}34 \times 5\text{--}8 \mu\text{m}$ distally; median cell shorter, $10\text{--}16 \times 5\text{--}8 \mu\text{m}$; upper cell shortest, $8\text{--}10 \times 5\text{--}8 \mu\text{m}$; antheridium $20\text{--}29 \times 6\text{--}9 \mu\text{m}$, one margin often more convex than the other. Total length 60–88 μm .

Female individual.—*Receptacle:* Like that of the monoecious form; 35–42 μm long; basal cell $15\text{--}20 \times 8\text{--}9 \mu\text{m}$ immediately below cells II and III; cell II $17\text{--}22 \times 8\text{--}10 \mu\text{m}$; cell III $20\text{--}25 \times 8\text{--}10 \mu\text{m}$, the upper part becoming separated from the lower part by a secondary cross wall, forming a basally rounded cell $12\text{--}17 \times 8\text{--}10 \mu\text{m}$.

Appendage: Consisting usually of two cells, the lower cell $12\text{--}18 \times 6\text{--}9 \mu\text{m}$; the upper cell $25\text{--}34 \times 6\text{--}9 \mu\text{m}$, rarely divided into two by a submedian cross wall. Total length 37–52 μm .

Perithecium: Like that of the monoecious form; stalk cell (VI) $20\text{--}31 \times 15\text{--}18 \mu\text{m}$; secondary stalk cell (VII) relatively short, 13–21 μm long; basal cell m 31–38 μm long; that part of the basal cell region composed of basal cells n' and n 15–25 μm long; stalk cells and basal cells forming a perithecial stipe 40–50 μm long by 17–20 μm wide at mid-height; body above the basal cells $110\text{--}140 \times 44\text{--}50 \mu\text{m}$. Ascospores $46\text{--}51 \times 5 \mu\text{m}$ (less sheath).

Total length from tip of foot to tip of perithecium 200–224 μm .

Etymology.—From *biformis* (L.), two formed.

Holotype.—PHILIPPINE ISLANDS: Luzon; Pampanga prov.; Angeles, 30 Oct. 1970, W. K. Reisen coll. (H-57-70). On the left margin of the abdomen near the tip of *Mesovelvia vittigera* Horv. (Fig. 46) (Hemiptera: Mesoveliidae); RKB 2846 (on 12 macropterous ♀♀, five apterous ♀♀, five macropterous ♂♂, and three apterous ♂♂); slides in RSA.

Other specimens examined.—PHILIPPINE ISLANDS: Luzon; Pampanga prov.; Arayat, 21 Feb. 1971, ?W. K. Reisen [collector's name not on label] (H-116-71). On various parts of *Mesovelvia vittigera*; RKB 2843 (on one macropterous ♀), RKB 2844 (on two apterous ♀♀), and RKB 2845B (on four apterous ♂♂); slides in RSA.

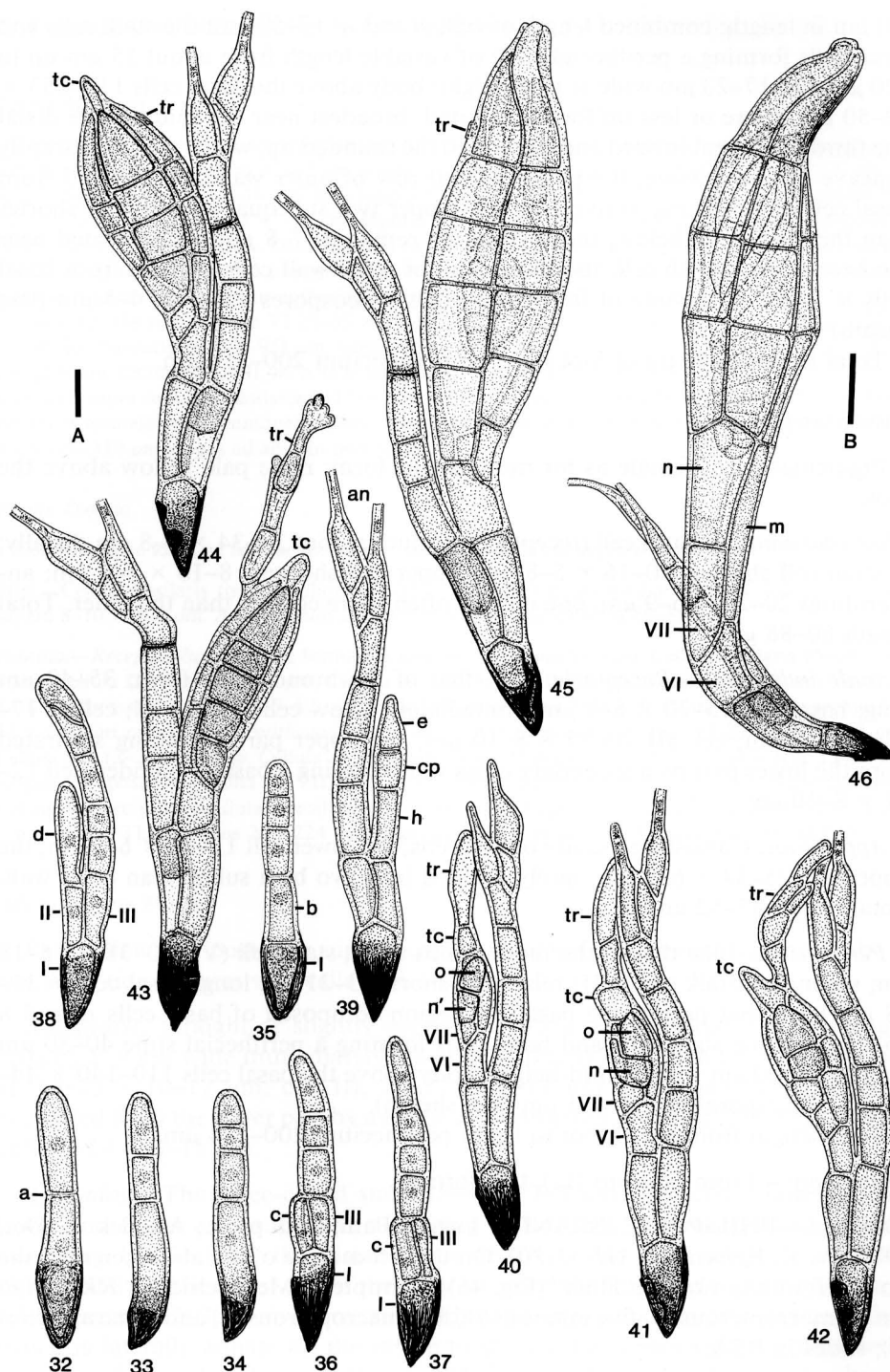


Fig. 32-46. *Triceromyces bififormis* (monoecious form) (RKB 2846).—32-45. Stages of development of the receptacle, appendage, and perithecium. Details and terminology are given in the text.—46. A mature individual showing the elongate perithecial stalk consisting of the primary and secondary stalk cells (VI, VII) and basal cells (*m*, *n*, and *n'* [far side]). (Fig. 32-45, bar A = 10 μ m; Fig. 46, bar B = 20 μ m.)

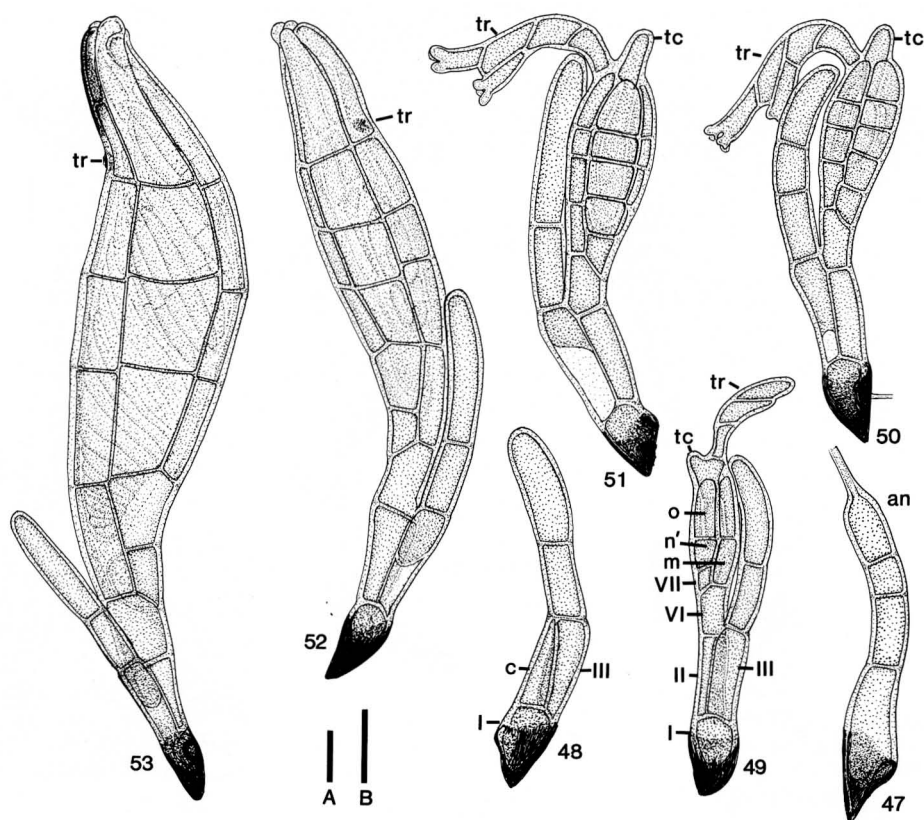


Fig. 47–53. *Triceromyces bififormis* (dioecious form) (Fig. 47–48, 50: RKB 2846; Fig. 49, 51–52: RKB 2845B; Fig. 53: RKB 2844).—47. A mature male individual showing the single terminal antheridium (an).—48–52. Several stages of development of the receptacle, appendage, and perithecium. Details and terminology are given in the text.—53. A mature female. (Fig. 47–52, bar A = 10 μ m; Fig. 53, bar B = 20 μ m.)

In all, fungi recovered from the above hosts included 66 specimens of the monoecious form (19 mature, 47 immature); 40 females of the dioecious form (11 mature, 29 immature); and 32 males. Male and female hosts, apterous or macropterous, were parasitized. In the Angeles collection, all individuals of the monoecious form (six mature, 31 immature) were found only on macropterous female hosts (all specimens on apterous females were too immature for categorization); nine female individuals of the dioecious form (five mature, four immature) were found only on male hosts; but of 20 male individuals of the dioecious form, 10 were found on female hosts and 10 on male hosts. In the Arayat collection, 29 monoecious forms (13 mature, 16 immature) were found on both female (20 thalli) and male (9 thalli) hosts; 31 females of the dioecious form (six mature, 25 immature) were found on both sexes of host (14 thalli on females, 17 thalli on males); and 12 male thalli of the dioecious form of the parasite likewise were found on both sexes of host (seven on females, five on males).

In the Arayat material, both monoecious and dioecious forms of the parasite were found growing, often together, in several different positions on the host—the upper and lower surfaces and lateral margins of the abdomen, on the head

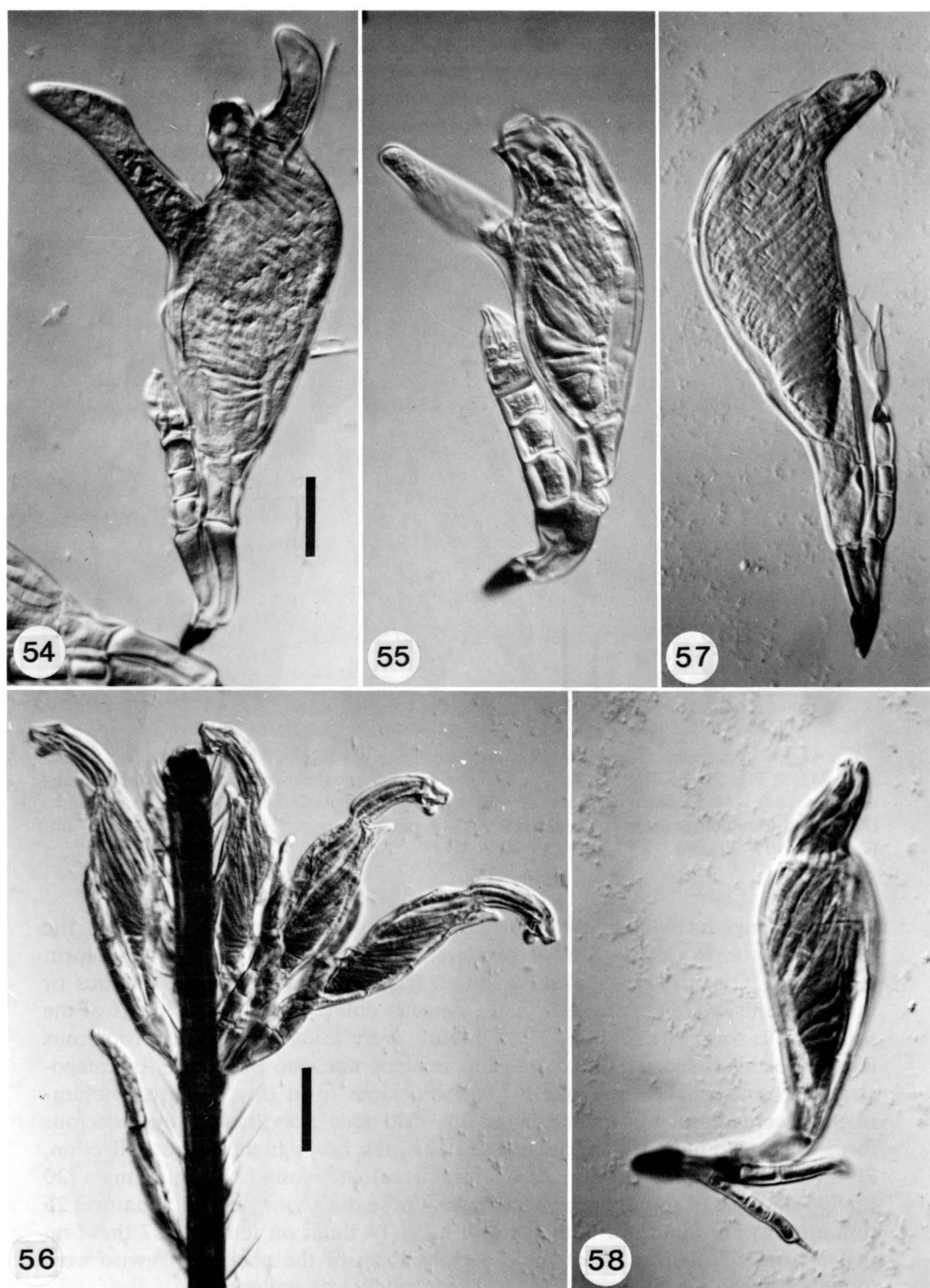


Fig. 54–58. *Triceromyces* species, mature individuals.—54. *Triceromyces balazucii* (Majewski 1584).—55. *Triceromyces hebri* (RKB 2703).—56. *Triceromyces hydrometrae* (RKB 2891). Four spec-

and pronotum, and on the legs. In the Angeles material, on the other hand, all of the fungi were found on the left margin of the last abdominal tergite (sternum VIII).

This species, like *T. bullatus* and *T. poissonii*, also found on Mesoveliidae, differs from the three species discussed above in having perithecia lacking outsized perithecial outgrowths and in the reduced number of antheridia formed on the primary appendage of the monoecious form. Only monoecious forms are known for the species on Hebridae and Hydrometridae in contradiction to the regular occurrence of both monoecious and dioecious forms in taxa found on Mesoveliidae.

Triceromyces biformis bears much resemblance to *T. poissonii*, especially in the characteristics of the monoecious form where slightly smaller dimensions of the appendage in *T. poissonii* serve to distinguish it from *T. biformis*. The dioecious forms of these species are readily separated by characteristics of the appendage, which is relatively long and slender in *T. biformis* and short and stout in *T. poissonii*.

5. *Triceromyces bullatus* Benjamin, sp. nov.

Fig. 59–66, 74–76, 83

Forma Monoeca

Receptaculum atroporphyreum. Superficies postica perithecii e basi stipitis ad apicem atroporphyrea; superficies antica perithecii e basi ad apicem pallide flavobrunnea. Appendix pro parte maxima pallide flavobrunnea; pars antheridiiferum prope basin porphyreum. *Receptaculum* leniter curvatum $48\text{--}52 \times 16\text{--}18 \mu\text{m}$. Cellula I $20 \times 10 \mu\text{m}$. Cellula II $25\text{--}32 \times 8\text{--}10 \mu\text{m}$. Cellula III $30\text{--}35 \times 7\text{--}10 \mu\text{m}$; pars superum cellulae cellulam $18\text{--}22 \times 7\text{--}10 \mu\text{m}$ formans. *Appendix* $116 \mu\text{m}$ longa. Stipes $39\text{--}47 \times 7 \mu\text{m}$; cellulae cylindricae; septum supernum fuscum. Cellulae basillares et terminales subaequales ($14\text{--}15\text{--}18 \mu\text{m}$ longae. Cellula media $10\text{--}13 \mu\text{m}$ longa. Pars antheridiiferum bicellulare; cellula infima elongata $22\text{--}23 \times 5 \mu\text{m}$ antheridium singulum erectum cellulae superae a latere adnatum gignens; cellula supra brevior antheridium singulum erectum liberum gignens. Antheridia $32\text{--}35 \times 4\text{--}4.5 \mu\text{m}$. *Perithecium*: Cellula VI $41\text{--}45 \times 13\text{--}14 \mu\text{m}$. Cellula VII $52\text{--}55 \mu\text{m}$ longa. Cellula *m* cellulae basillares $89\text{--}92 \mu\text{m}$ longa. Pars ex cellulis basillaribus *n* et *n'* ca. $45 \mu\text{m}$ longum compositum. Cellulae VI, VII, *m*, *n*, et *n'* stipitem perithecialem $123\text{--}137 \times 13\text{--}15 \mu\text{m}$ facientes. Corpus perithecii supra cellulam basillarem $165\text{--}168 \times 50 \mu\text{m}$ plus minusve uniformiter inflatum. Apex perithecii rotundatum plerumque parum inflexus. Cellulae extimae una duae et tres serierum cellulosarum ex *m*-cellula basillari et *n*-cellula basillari contigui oriundae bullatae; bullae in seriebus longitudinalibus dispositae. Cellulae extimae ceterae laeves. Ascospores hyalinae $48\text{--}51 \times 4\text{--}5 \mu\text{m}$ (sine vagina). Thallus totus $345\text{--}355 \mu\text{m}$ longus ad apicem perithecii (aestimatus).

Forma Dioecia

Color feminae idem ac formae monoecae; appendix pallide flavobrunnea. Mas hyalinus supra pedem.

Mas.—Cellula basillaris (receptaculum) $30\text{--}33 \times 6\text{--}7 \mu\text{m}$. Cellula media $10\text{--}11 \times 6 \mu\text{m}$. Cellula supra $7\text{--}8 \times 6 \mu\text{m}$. Antheridium $19\text{--}20 \times 6\text{--}7 \mu\text{m}$. Thallus totus $66\text{--}70 \mu\text{m}$.

Femina.—*Receptaculum* idem ac formae monoecae $44\text{--}46 \mu\text{m}$ longa. Cellula I $17\text{--}20 \times 10 \mu\text{m}$. Cellula II $21\text{--}25 \times 8\text{--}10 \mu\text{m}$. Cellula III $23\text{--}26 \times 10 \mu\text{m}$; pars superum cellulae cellulam $15 \times 10 \mu\text{m}$ formans.

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imens on fragment of host antenna.—57–58. *Triceromyces biformis* (RKB 2846).—57. Monoecious form.—58. Dioecious form showing paired female and male individuals. (Fig. 54–55, 57–58, bar with Fig. 54 = $30 \mu\text{m}$; Fig. 56, bar = $50 \mu\text{m}$.)

Appendix 23–25 μm longa. Cellula infima 9–11 \times 7 μm . Cellula suprema 12–15 \times 7 μm . *Perithecium* idem ac formae monoecae. Cellula VI 33 \times 15 μm . Cellula VII 60 μm longa. Cellula *m* 80 μm longa. Pars ex cellulis basilaribus *n* et *n'* 40 μm longum compositum. Cellulae VI, VII, *m*, *n*, et *n'* stipitem perithecialem 120 \times 15 μm facientes. Corpi perithecii supra cellulam basilem 165 \times 44 μm . Ascosporeae non observatae. Thallus totus 320 μm longum ad apicem perithecii. Typus *RKB 2845A* (RSA).

Monoecious Form

Receptacle and posterior surface of the perithecium from base of stipe to tip deep reddish brown; anterior surface of the perithecium from base of stipe to tip pale yellowish brown; appendage pale yellowish brown, except for the lower end of the basal cell of the antheridiiferous part, which is reddish brown.

Receptacle: Slightly curved, 48–52 \times 16–18 μm ; basal cell 20 μm long by 10 μm wide immediately below cells II and III, which are subequal; cell II 25–32 \times 8–10 μm ; cell III 30–35 \times 7–10 μm , the upper part becoming separated from the lower part by a secondary cross wall, forming a basally rounded cell 18–22 \times 7–10 μm .

Appendage: The three-celled stalk 39–47 \times 7 μm ; the cells cylindrical; the lower and upper cells subequal, (14–)15–18 μm long; the median cell slightly shorter, 10–13 μm long; the distal antheridiiferous part consisting of two elongate superposed cells, separated from the upper end of the stalk by a darkened septum; the lower cell 22–23 \times 5 μm , subtending an upwardly directed antheridium, which is laterally adnate on the inside to the slightly shorter upper cell, which subtends a free antheridium; antheridia 32–35 \times 4–4.5 μm . Total length to tip of upper antheridium 116 μm .

Perithecium: Stalk cell (VI) slender, 41–45 \times 13–14 μm ; secondary stalk cell (VII) slender, elongate, 52–55 μm long, as is basal cell *m*, which is 89–92 μm in length; combined length of basal cells *n* and *n'* ca. 45 μm ; the stalk cells and basal cells forming a slender perithecial stipe, broadest above, 123–137 μm long by 13–15 μm wide at mid-height; body above the basal cells 165–168 \times 50 μm , uniformly inflated, broadest near the middle, the tapered apex inclined inward slightly; the tip narrow, rounded; the anterolateral row of outer wall cells derived from basal cell *m* consisting of five cells, the apical cell slightly shorter than the subapical, which bears near its base the more or less protrudent trichogynic remnant; the three rows of outer wall cells derived from basal cells *n* and *n'* consisting of four (?five) cells; the lower three outer wall cells derived from basal cell *m* and the adjacent row derived from basal cell *n* bullate, the rounded prominences disposed in more or less vertical rows; the other row of outer wall cells derived from basal cell *n* and the adjacent row derived from basal cell *n'* smooth. Ascospores 48–51 \times 4–5 μm (less sheath).

Total length from tip of foot to tip of perithecium 345–355 μm (estimated).

Dioecious Form

Pigmentation of the receptacle and perithecium of the female as for the monoecious form; appendage pale yellow brown; male hyaline above the dark brown foot.

Male individual.—Basal cell (receptacle), including foot, $30\text{--}33 \times 6\text{--}7\ \mu\text{m}$ distally; median cell shorter, $10\text{--}11 \times 6\ \mu\text{m}$; upper cell shortest, $7\text{--}8 \times 6\ \mu\text{m}$; antheridium $19\text{--}20 \times 6\text{--}7\ \mu\text{m}$, one margin slightly more convex than the other. Total length $66\text{--}70\ \mu\text{m}$.

Female individual.—*Receptacle*: Like that of the monoecious form; $44\text{--}46\ \mu\text{m}$ long; basal cell $17\text{--}20 \times 10\ \mu\text{m}$; cell II, $21\text{--}25 \times 8\text{--}10\ \mu\text{m}$; cell III, $23\text{--}26 \times 10\ \mu\text{m}$, the upper part becoming separated from the lower part by a secondary cross wall, forming a basally rounded cell $15 \times 10\ \mu\text{m}$.

Appendage: Consisting of two subequal superposed cells; the lower cell $9\text{--}11 \times 7\ \mu\text{m}$; the upper cell, rounded apically, $12\text{--}15 \times 7\ \mu\text{m}$. Total length $23\text{--}25\ \mu\text{m}$.

Perithecium: Nearly identical to that of the monoecious form; stalk cell (VI) $33 \times 15\ \mu\text{m}$; secondary stalk cell (VII) $60\ \mu\text{m}$ long; basal cell $m\ 80\ \mu\text{m}$ long; combined length of basal cells n and n' $40\ \mu\text{m}$; stalk cells and basal cells forming a perithecial stipe $120\ \mu\text{m}$ long by $15\ \mu\text{m}$ wide at mid-height; body above basal cells $165 \times 44\ \mu\text{m}$. Ascospores not observed.

Total length from tip of foot to tip of perithecium $320\ \mu\text{m}$.

Etymology.—From *bullatus* (L.), bullate; named for the distinctive external modification of two rows of outer wall cells.

Holotype.—PHILIPPINE ISLANDS: Luzon; Pampanga prov., Arayat, 21 Feb. 1971, ?W. K. Reisen [collector's name not on label] (*H-116-71*). On the femur of the left middle and anterior legs of *Mesovelia vittigera* (Fig. 59, 74); *RKB 2845A* (on three apterous ♂♂); slides in RSA.

Both monoecious and dioecious forms of *T. bullatus* were closely associated on the legs of the hosts. Only a few specimens of the parasite were recovered: for the monoecious form—two mature, but broken, individuals (Fig. 59–60, 74, 83), two immature individuals (Fig. 62), and one mature receptacle with intact antheridial appendage (Fig. 61); for the dioecious form—one mature female (Fig. 64, 75), one immature female (Fig. 63), one receptacle with intact appendage, and six males (Fig. 65–66, 76). Despite the small number of specimens available for study, the taxon could be readily defined, although dimensions given in the description doubtless will need emendation when additional specimens of the species are discovered. Because of the characteristic morphology of the perithecium of both the monoecious and dioecious forms, *T. bullatus* is clearly distinct from its congener, *T. bififormis*, growing on the same host.

6. *Triceromyces poissonii* (Benjamin) Benjamin, comb. nov. Fig. 67–73, 77–80, 84–88

≡ *Autophagomyces poissonii* Benjamin, Aliso 7:167, 1970 (monoecious form).

= *Dioicomyces mesoveliae* Benjamin, Aliso 7:172, 1970 (dioecious form).

Monoecious Form

Receptacle, especially the upper part of cell III, suffused with dark reddish brown, as is the lower end of the basal cell of the antheridiiferous part of the

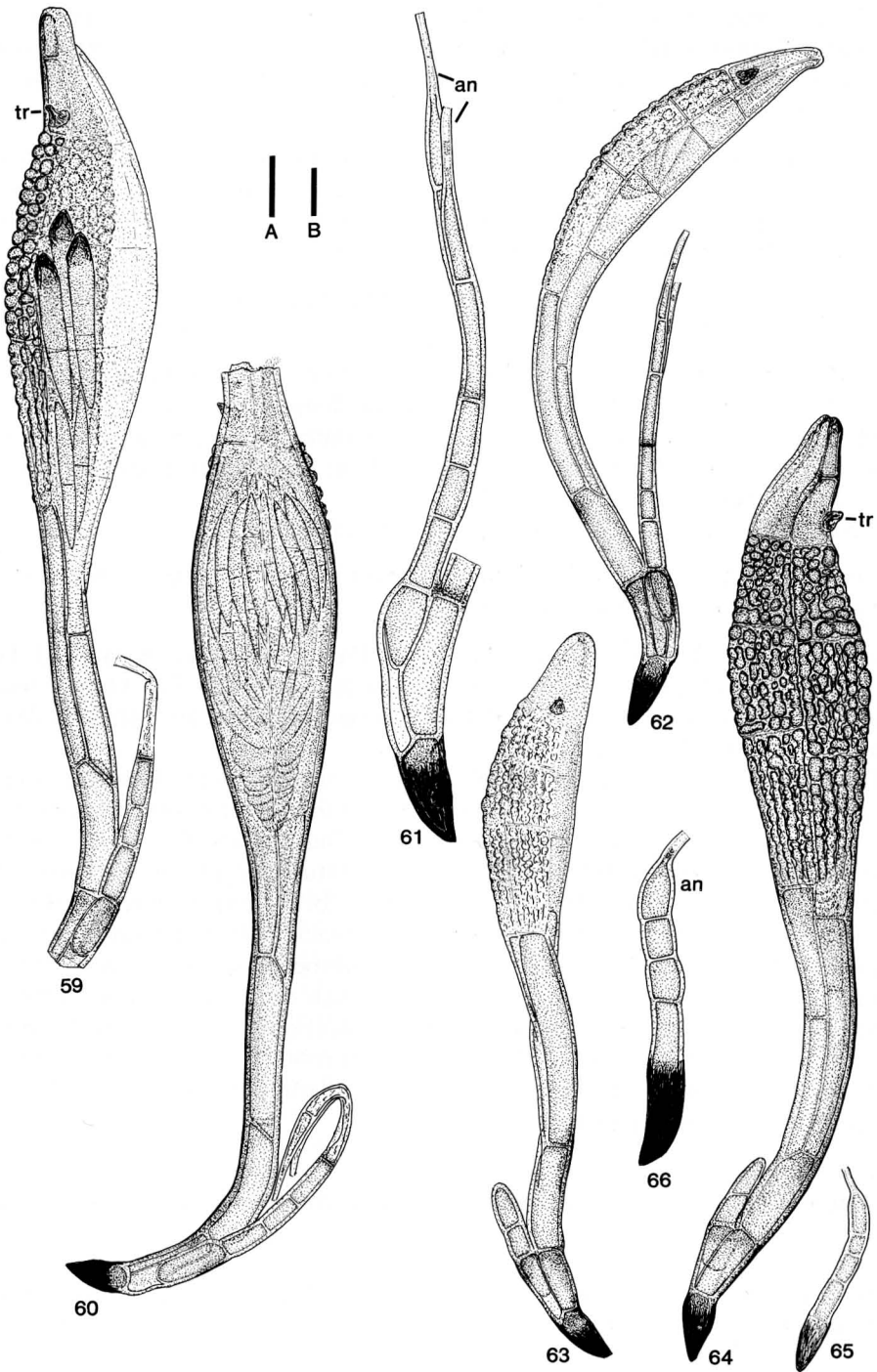


Fig. 59–66. *Triceromyces bullatus* (RKB 2845A).—59–62. Monoecious form.—59–60. Two mature, but broken, individuals. The perithecium of the specimen depicted in Fig. 59 is shown in near view and optical section; see Fig. 74 for a view of the far surface of the same perithecium. The perithecium of the specimen depicted in Fig. 60 is shown in near view and optical section; see Fig.

appendage; perithecium pale yellowish to yellowish brown except for the posterior surface near the tip, which is dark reddish brown.

Receptacle: Straight to slightly curved, $48\text{--}55 \times 21\text{--}25\text{ }\mu\text{m}$ distally; basal cell (I) nearly obscured by the dark suffusion of the foot, $17\text{--}22\text{ }\mu\text{m}$ long by $10\text{--}11\text{ }\mu\text{m}$ wide immediately below cells II and III; cell II $25\text{--}32 \times 9\text{--}12\text{ }\mu\text{m}$; cell III $30\text{--}40 \times 11\text{--}15\text{ }\mu\text{m}$, the upper part becoming separated from the lower part by a secondary cross wall, forming a basally rounded cell $17\text{--}23 \times 11\text{--}15\text{ }\mu\text{m}$.

Appendage: The three-celled stalk $30\text{--}34(\text{--}40)\text{ }\mu\text{m}$ long; the cells cylindrical; the lower cell slightly longer than broad, $10\text{--}15 \times 10\text{--}12\text{ }\mu\text{m}$; the median cell isodiametric, $8\text{--}10 \times 8\text{--}10\text{ }\mu\text{m}$; the upper cell longer than broad, $11\text{--}14 \times 7\text{--}10\text{ }\mu\text{m}$; axis of the distal antheridiiferous part consisting of two cells, separated from the upper cell of the stalk by a darkened septum; the lower cell about twice as long as broad, $15\text{--}17 \times 7\text{--}10\text{ }\mu\text{m}$, subtending an upwardly directed antheridium, which is laterally adnate on the inside to the smaller upper cell; the latter cell subtending a free antheridium; antheridia $25\text{--}30 \times 7\text{--}10\text{ }\mu\text{m}$. Total length to tip of upper antheridium $75\text{--}95\text{ }\mu\text{m}$.

Perithecium: Stalk cell (VI) slightly longer than broad, $25\text{--}30 \times 18\text{--}23\text{ }\mu\text{m}$; secondary stalk cell (VII) variable, $25\text{--}30\text{ }\mu\text{m}$ in length, as is basal cell *m*, which ranges from 48 to $75\text{ }\mu\text{m}$ in length; that part of the basal cell region comprised of basal cells *n* and *n'* $25\text{--}35\text{ }\mu\text{m}$ in length; the stalk cells and basal cells forming a stipe of variable length $70\text{--}115\text{ }\mu\text{m}$ long by $18\text{--}25\text{ }\mu\text{m}$ wide at mid-height; body above the basal cells $118\text{--}144 \times 42\text{--}50\text{ }\mu\text{m}$, more or less uniformly inflated, broadest near the middle, the distal one third usually bent inward slightly and tapered to the rounded tip, which may be abruptly concave on the outer margin; the posterolateral row of outer wall cells derived from basal cell *m* consisting of five cells, with the terminal cell slightly shorter than the subterminal cell, which bears the trichogynic remnant near the base; the three rows of outer wall cells derived from basal cells *n* and *n'* consisting of four (?five) cells. Ascospores $42\text{--}46 \times 5\text{--}6\text{ }\mu\text{m}$ (less sheath).

Total length from tip of foot to tip of perithecium $240\text{--}300\text{ }\mu\text{m}$.

Dioecious Form

Pigmentation of the receptacle and perithecium as in the monoecious form; appendage pale yellowish brown to dark reddish brown. Male nearly hyaline above the brownish-black foot.

Male individual.—Basal cell (receptacle), including foot, $30\text{--}36 \times 6\text{--}8\text{ }\mu\text{m}$ distally; median and upper cells subequal, the former $8\text{--}10 \times 6\text{--}8\text{ }\mu\text{m}$, the latter $6\text{--}8 \times 7\text{--}8\text{ }\mu\text{m}$; antheridia $20\text{--}29 \times 7\text{--}10\text{ }\mu\text{m}$, usually slightly more convex on one side than the other. Total length $66\text{--}80\text{ }\mu\text{m}$.

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83 for a view of the far surface of the same perithecium.—61. Mature receptacle with intact appendage bearing two elongate antheridia (*an*).—62. Young individual.—63–66. Dioecious form.—63. Young female.—64. Mature female near view of bullate perithecial wall (see also Fig. 75).—65–66. Mature males showing single terminal antheridia (*an*). (Fig. 59–60, 62–65, bar A = $20\text{ }\mu\text{m}$; Fig. 61, 66, bar B = $10\text{ }\mu\text{m}$.)

Female individual.—*Receptacle*: Like that of the monoecious form; $45\text{--}56 \times 21\text{--}25\text{ }\mu\text{m}$ distally; basal cell (I) nearly obscured by the brownish-black foot, $19\text{--}22\text{ }\mu\text{m}$ long by $9\text{--}12\text{ }\mu\text{m}$ wide immediately below cells II and III; cell II $24\text{--}30 \times 10\text{--}13\text{ }\mu\text{m}$; cell III $29\text{--}35 \times 12\text{--}16\text{ }\mu\text{m}$, the upper part becoming separated from the lower part by a secondary cross wall, forming a basally rounded cell $16\text{--}23 \times 12\text{--}16\text{ }\mu\text{m}$.

Appendage: Consisting usually of two cells; the lower cell about half the length of the upper cell and slightly wider, $9\text{--}13 \times 10\text{--}15\text{ }\mu\text{m}$; the upper cell broadest at the base, rounded at the tip, $16\text{--}24 \times 9\text{--}13\text{ }\mu\text{m}$, rarely divided in two by a submedian cross wall. Total length $26\text{--}35\text{ }\mu\text{m}$.

Perithecium: Like that of the monoecious form; stalk cell (VI) $28\text{--}44 \times 18\text{--}22\text{ }\mu\text{m}$; secondary stalk cell (VII) variable, $37\text{--}108\text{ }\mu\text{m}$ long; basal cell *m* variable, $48\text{--}144\text{ }\mu\text{m}$ long; that part of the basal cell region comprised of basal cells *n* and *n'* $20\text{--}50\text{ }\mu\text{m}$ long; stalk and basal cells forming a perithecial stipe of variable length $78\text{--}162\text{ }\mu\text{m}$ long by $18\text{--}26\text{ }\mu\text{m}$ wide at mid-height; body above the basal cells $122\text{--}180 \times 44\text{--}56\text{ }\mu\text{m}$. Ascospores $43\text{--}55 \times 5\text{--}7\text{ }\mu\text{m}$ (less sheath).

Total length from tip of foot to tip of perithecium $235\text{--}385\text{ }\mu\text{m}$.

Specimens examined.—In preparing the above description, I reexamined the specimens studied when I originally characterized *Autophagomyces poissonii* (RKB 2075B,C, which included the type, on a macropterous ♂ from Georgetown, Texas) and *Dioicomyces mesoveliae* (RKB 2080, which included the type, on a macropterous ♂ from Oaxaca, Mexico; 2075A on four macropterous ♂♂ from Georgetown, Texas; 2566 on an apterous ♂ from Rivas, Nicaragua; and 2567 on two macropterous ♂♂ from the state of Michoacan, Mexico) (for details see Benjamin 1970). The host in all cases was *Mesovelia mulsanti* White (Hemiptera: Mesoveliidae). Additional specimens studied were as follows: MEXICO: Jalisco; 10 mi N of Chapala, 22 Apr. 1964, J. T. and M. S. Polhemus coll. (CL 1031). On the upper and lower surface of the abdomen and on the legs of *M. mulsanti*; RKB 2839 (on one macropterous ♀ and one apterous ♀), 2840 (on one macropterous ♂); slides in RSA.—Durango, Peñon Blanco, 1 Aug. 1952, J. D. Lattin coll. [leg. J. T. Polhemus]. On the upper and lower surface of the abdomen and on the legs of *M. mulsanti*; RKB 2841 (on one macropterous ♂), 2842 (on three apterous ♀♀); slides in RSA.

Specimens of *Triceromyces poissonii* recovered from the above hosts included 48 specimens of the monoecious form (six mature, 42 immature) and 81 females of the dioecious form (53 mature or nearly mature, 31 immature) together with 55 males. The monoecious form was found most commonly on female hosts (the collections from Peñon Blanco and Chapala, Mexico, and Georgetown, Texas), but it did occur, in two instances, on male hosts, one from Jalisco, Mexico, and one from Georgetown. The dioecious form was found exclusively on male hosts.

In most cases, the dioecious form was found on the legs of the host (RKB 2075A, 2080, 2566, 2567, 2840, 2841). The monoecious form was found on the upper surface of the abdomen of female hosts (RKB 2839, 2842), but it was found on the legs of two males (RKB 2075B,C, 2840).

The close resemblance of *T. poissonii* and *T. bififormis*, especially the monoecious forms, already has been mentioned under the latter species. The two taxa are most readily distinguished on the basis of the appendage of the females of their dioecious forms.

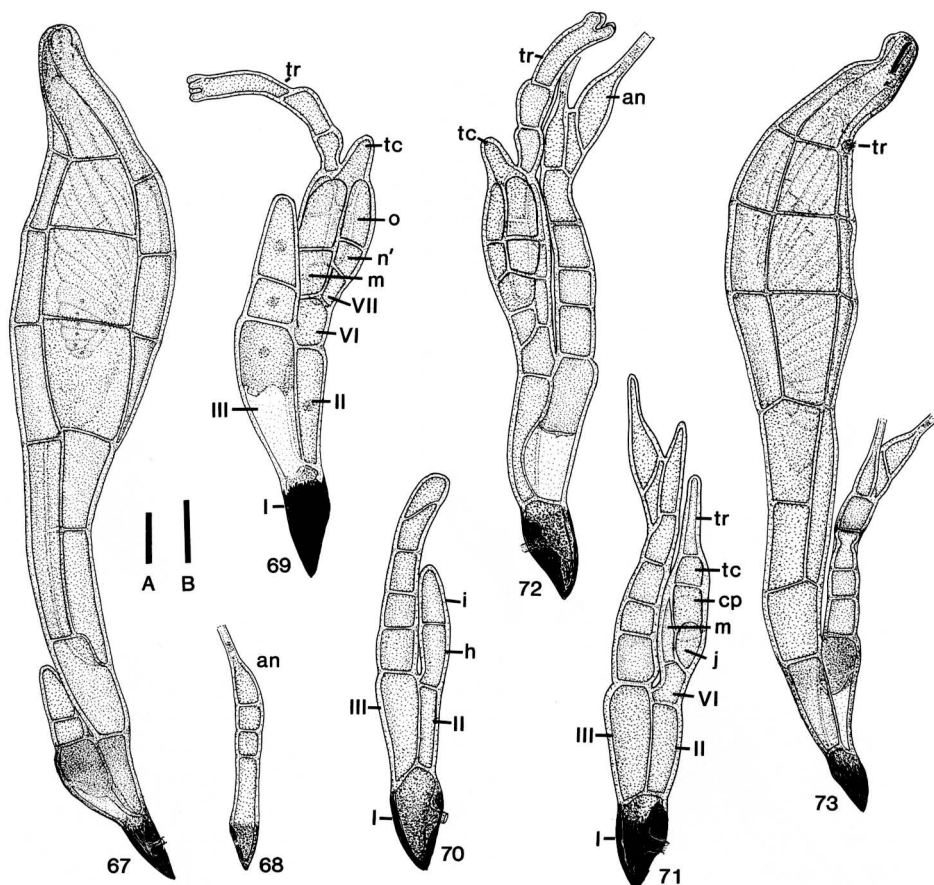


Fig. 67–73. *Triceromyces poissonii*.—67–69. Dioecious form (Fig. 67, 69: RKB 2841; Fig. 68: RKB 2840).—67. Mature female.—68. Mature male showing single terminal antheridium (*an*).—69. Immature female; see text for details and terminology, and for a photograph of this specimen see Fig. 86.—70–73. Monoecious form (RKB 2839).—70–72. Three young individuals showing stages of development of the receptacle, appendage, and perithecium; see text for details and terminology.—73. Mature individual. (Fig. 69–72, bar A = 10 μ m; Fig. 67–68, 73, bar B = 20 μ m.)

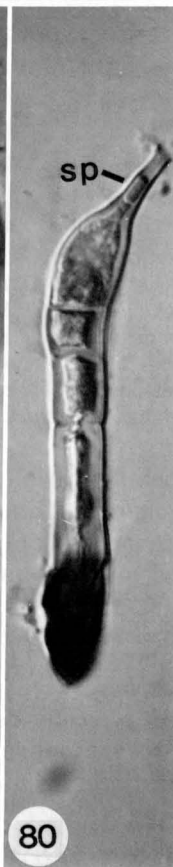
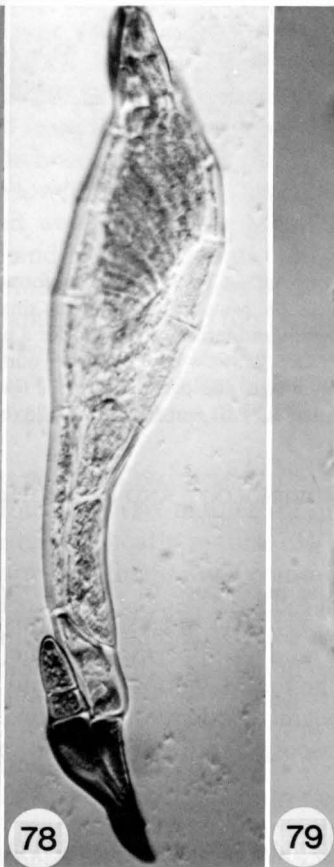
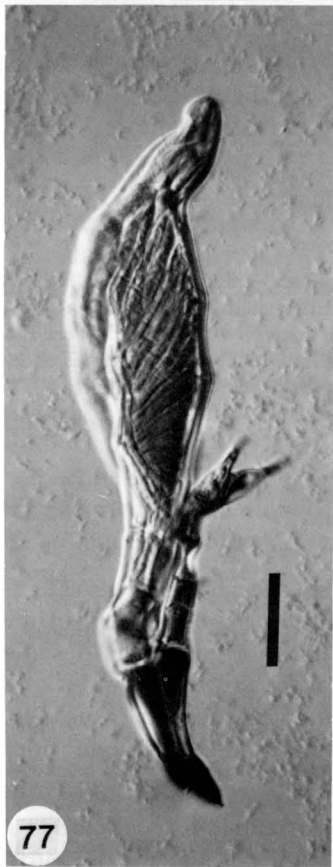
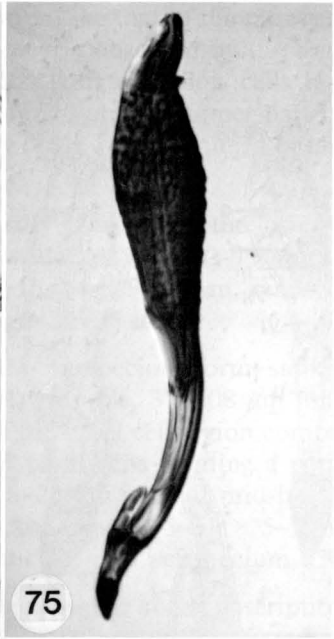
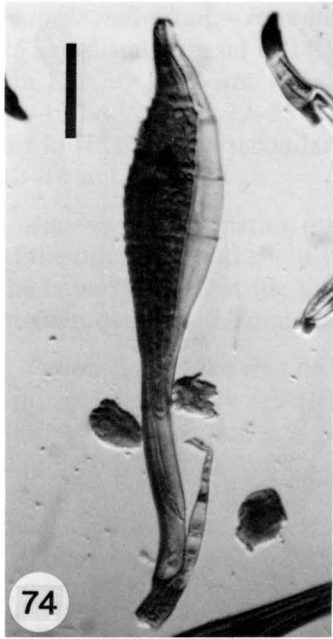
MORPHOLOGY AND DEVELOPMENT

Ascospores

The septum dividing the ascospore of *Triceromyces* species into two cells is submedian (Fig. 4–5, 13, 31). The longest cell constitutes 55–60 percent of the total length of the spore and is uppermost in the perithecium prior to spore discharge (Fig. 60, 81). The foot develops at the end of the longer cell and it can, but typically does not, begin to differentiate prior to spore discharge (Fig. 59). Asci are four spored. No ascosporic dimorphism is apparent in either monoecious or dioecious morphs.

Monoecious Forms and Female Individuals of Dioecious Forms

Receptacle.—In one of the earliest stages of development observed, shown in Figures 14 and 32, the lower end of the basal cell of the spore, separated from



the upper cell by the original cross wall (*a*), has differentiated the foot, which is darkly pigmented. Early divisions of the upper spore segment leading to development of the primary appendage (Fig. 15–16, 33–34) appear to take place before formation of a transverse cross wall separating the basal cell of the spore into a lower cell, the true basal cell (I) of the receptacle, and an upper cell (*b*) subtending the young appendage (Fig. 35). The upper cell then is divided by a nearly vertical cross wall, which delimits cells *c* and III of the young receptacle (Fig. 17–18, 36–37, 48). Cell *c* is broadest at the base at this stage of development, whereas cell III, the true terminal cell of the receptacle, is broadest distally where it subtends the appendage. Cell *c* soon gives rise from its upper angle to the perithecial initial (*d*) and becomes cell II, the true subbasal cell of the receptacle (Fig. 19–20, 38).

In addition to enlargement of cells II and III to definitive size, there is a further modification of cell III as growth progresses. Concomitant with maturation of the appendage and development of the young perithecium, the cytoplasm of cell III becomes concentrated in the upper part of the cell, leaving a void in the lower part (Fig. 6–8, 22, 43–44, 50–51, 69, 72, 86). This cytoplasm, containing a single nucleus (Fig. 86), then is isolated from the lower part of the cell by a secondarily formed wall (Fig. 10–12, 23, 30, 45–46, 52–53, 59–64, 67, 73, 82, 84, 87–88).

Primary appendage.—The upper segment of the ascospore giving rise to female forms typically divides only once, forming a two-celled, sterile appendage (Fig. 48–49, 51–53, 58, 63–64, 67, 69, 75, 78, 86, 88). Infrequently, however, the upper cell of the appendage divides, which results in a three-celled appendage (Fig. 50, 87). Three-celled rather than two-celled appendages were found on three of 40 females of *T. biformis* and on four of 81 females of *T. poissonii*. Appendages on the three females of *T. bullatus* that were observed were two celled.

In monoecious forms, the first stage of development of the appendage from the upper cell of the spore also is marked by the formation of a transverse septum, which divides the cell into two more or less equal cells (Fig. 15, 32). The next division appears to take place in the upper cell followed by some elongation of the appendage (Fig. 16, 34–35). Only in *T. hydrometrae* does a remnant of the original spore apex persist on the upper cell as a short lateral spine (Fig. 16), which often is visible on the basal cell of the antheridiiferous part of the appendage (Fig. 17–18, 20, 22, 29). As the appendage elongates, the next stage of development probably involves a division of the lower cell (Fig. 17–18, 37), for the position of the lateral spine on the elongating terminal cell of individuals shown in Figures 17–18 is nearly the same as that shown in Figure 16. As growth of the thallus continues, the three lower cells of the appendage remain unchanged, except for enlargement, and constitute the stalk of the appendage (Fig. 3, 10, 23, 43, 61, 72).

Fig. 74–80. —74–75. *Triceromyces bullatus* (RKB 2845A). —74. Mature monoecious form (see also Fig. 59). —75. Mature female of dioecious form (see also Fig. 64). —76. Mature male. —77–80. *Triceromyces poissonii*. —77. Mature monoecious form (RKB 2839). —78. Mature female of dioecious form (RKB 2841). —79. Immature male prior to differentiation of the terminal antheridium (RKB 2480). —80. Mature male showing antheridium with a spermatium (*sp*) in the discharge tube (RKB 2480). (Fig. 74–75, bar with Fig. 74 = 50 μ m; Fig. 77–78, bar with Fig. 77 = 30 μ m; Fig. 76, 79–80, bar with Fig. 76 = 10 μ m.)

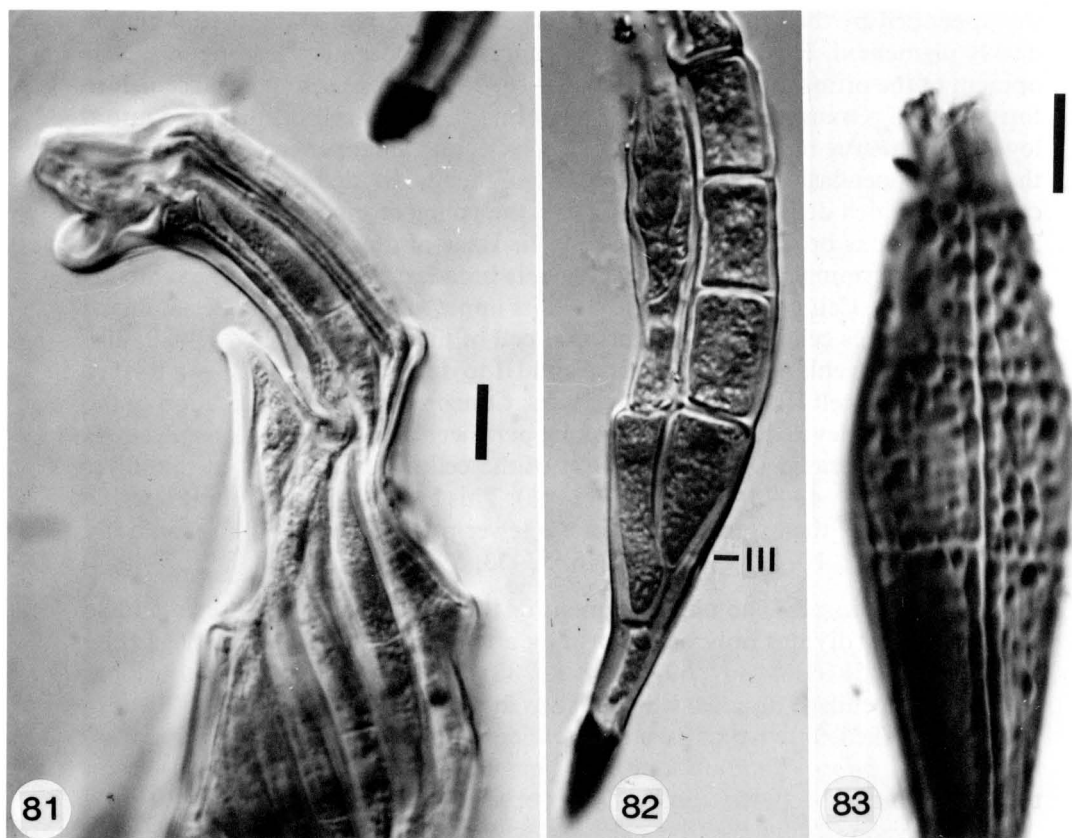


Fig. 81–83.—81–82. *Triceromyces hydrometrae*.—81. Upper half of a mature perithecium showing ascospores, the bluntly rounded perithecial upgrowth, and the basally constricted, narrow, curved, posteriorly lobate perithecial neck (RKB 2891).—82. Immature individual, less terminal part of appendage, showing the receptacle and the three-celled stalk of the appendage. Note modification of cell III of the receptacle, which has been divided by a secondarily formed wall into an upper living cell and a lower, slender, empty segment (RKB 2890).—83. *Triceromyces bullatus*. Body of a perithecium (tip broken) focused on far side to show bullations on outer wall cells derived from basal cells *m* and *n* (see also Fig. 60) (RKB 2845A). (Fig. 81–82, bar with Fig. 81 = 10 μ m; Fig. 87, bar = 20 μ m.)

The cross wall separating the upper cell of this stalk from the lower cell of the distal part eventually becomes more or less darkly pigmented externally (Fig. 1–3, 8, 10–12, 23, 29–30, 43–46, 59–62, 73).

After an appendage has reached the four-cell stage of development shown in Figures 17–18 and 37, the upper cell evidences the first step in the formation of the antheridiiferous part with the appearance of a diagonal cross wall separating it into two cells (Fig. 19, 38, 70). In *T. biformis*, *T. bullatus*, and *T. poissonii* each of these cells gives rise to a single antheridium (*an*) distally (Fig. 39–46, 61–62, 71–72). In *T. balazucii* and *T. hebri* the lower cell forms but one antheridium whereas the upper cell forms two (Fig. 1–3, 6–12); the three antheridia are basally united with only the efferent tubes being free. In *T. hydrometrae*, on the other hand, a succession of 4–7 cells is formed (Fig. 20–22), each cell growing upward and outward and cutting off a single free antheridium (Fig. 23, 29–30). In addition,

the upper cell develops a terminal, slender prolongation (Fig. 23, 29–30), which commonly is broken in older individuals.

The appendage of a monoecious form, with its complement of antheridia, appears always to be mature in advance of maturation of the trichogyne (Fig. 7–9, 23, 39–42, 71–72).

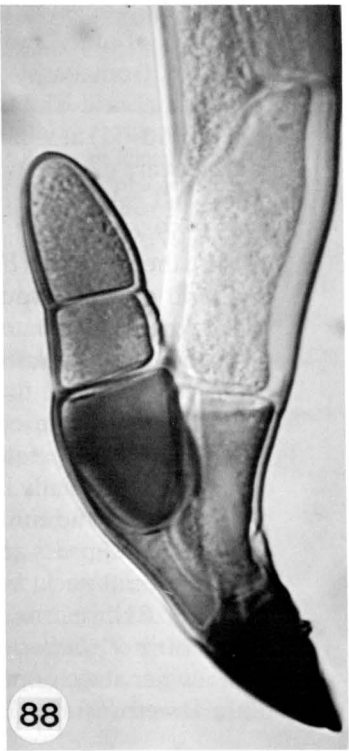
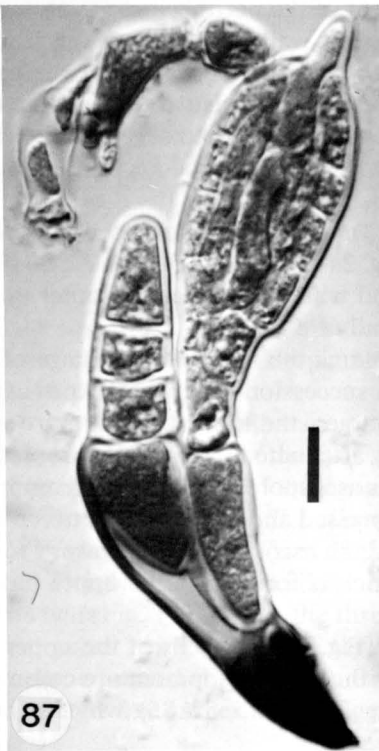
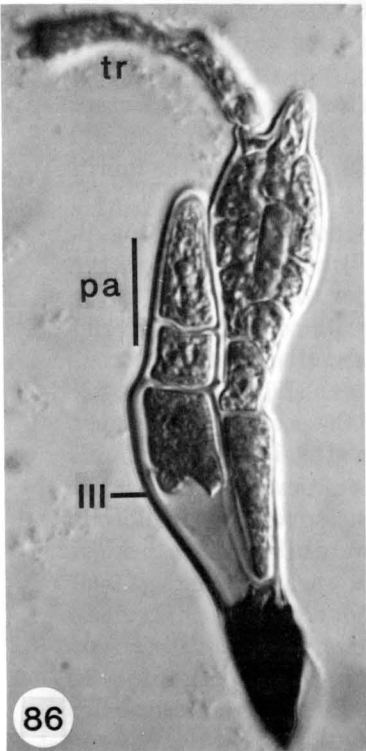
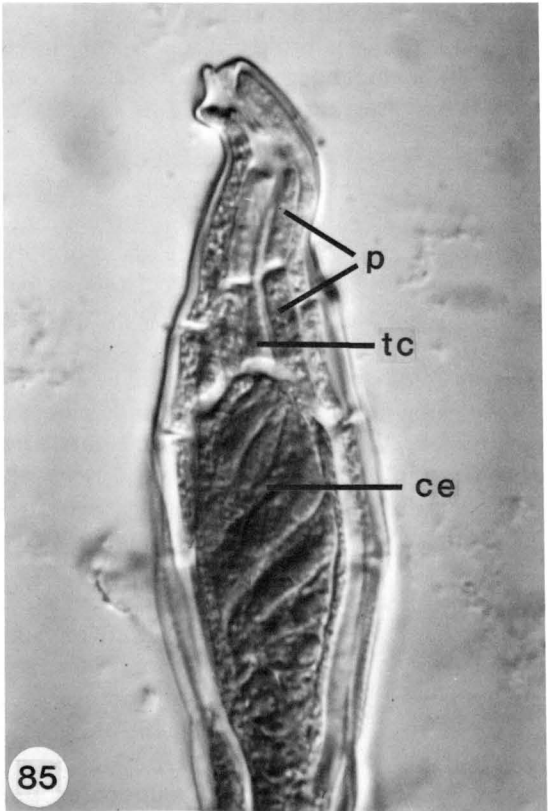
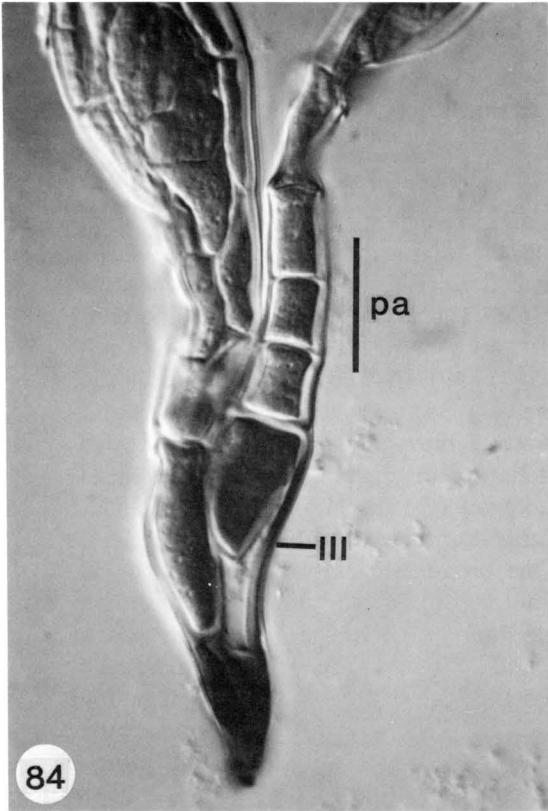
Perithecium.—The perithecial initial, *d* (Fig. 19–20, 38), divides and gives rise to the primordial cell of the perithecium (*h*) and the primordial cell of the procarp (*i*) (Fig. 21, 70). Cell *h* cuts off an upper cell *j* and a lower cell *k* (Fig. 6, 22), which then gives rise above to perithecial basal cell *m* (Fig. 7, 71) and becomes the primary stalk cell (VI) of the perithecium. Cell *j* gives rise, first on one side then the other, to perithecial basal cells *n* and *n'* and becomes the secondary stalk cell (VII) of the perithecium (Fig. 8, 23–24, 40–41, 49). Cell *i* divides and forms the carpogonial cell (*cp*) below and cell *e* above (Fig. 39), which, in turn, divides and gives rise to the trichophoric cell (*tc*) below and the young trichogyne (*tr*) above (Fig. 23, 71). While the first outer wall cells (*o*) are developing from the basal cells (*m*, *n*, *n'*), the trichogyne continues to grow (Fig. 8, 24, 40–41, 49, 69, 72).

Trichogynes were not found in *T. bullatus*, and mature trichogynes were not observed in *T. balazucii* and *T. hebri*. One broken, immature specimen of *T. balazucii* bore a trichogyne in about the same stage of development as those shown for *T. hebri* in Figures 8–9, which resemble the one shown for *T. hydrometrae* in Figure 24. In *T. hydrometrae*, *T. biformis*, and *T. poissonii* the mature trichogyne appears usually to consist of four superposed cells, with the subbasal cell giving rise to a one-celled divergent branch, which may be more or less adnate to the cell above (Fig. 25–26, 42, 50–51, 87). The tip of the terminal cell and branch forms a crown of short, rounded prominences.

Continued development of the perithecium involves the upward growth of the four rows of inner and outer wall cells (one row each from basal cells *m* and *n'*; two rows from basal cell *n*) and elaboration of the centrum derived from the carpogonial cell. The trichogyne persists to at least the three outer wall cell stage (Fig. 25, 50–51) at which time it begins to degenerate (Fig. 10, 43, 87). Eventually it disappears except for an often conspicuous remnant near the base of the fourth outer wall cell of the row derived from basal cell *m* (Fig. 2, 12, 27–30, 44–45, 52–53, 59–60, 62–65, 73). The trichophoric cell initially grows outward (Fig. 9, 41, 49), then upward (Fig. 24–27, 42–44, 50–51, 72, 86–87), and it appears to serve as a kind of guide around which the inner and outer upper wall cells grow as the trichogyne deflects laterally.

As the perithecium attains the four wall cell stage of development, the ascogenous cell gives rise to a succession of upwardly moving asci (Fig. 29, 45, 52, 62, 85). As the centrum enlarges, the lower tier and part of the second tier of inner wall cells become greatly attenuated from being compressed against the outer wall cells (Fig. 85). Finally, as ascospores mature, the remnant of the trichophoric cell, which has become compressed and attenuated between the upper, inner wall cells (Fig. 85), disappears and the ascospores pass upward towards the ostiole through the perithecial neck, which is formed by the upper outer and inner tiers of wall cells (Fig. 81).

Except in *T. bullatus* (Fig. 62–63), cells of the upper tier of outer wall cells at the four tier stage of perithecial development are commonly longer than the cells of the lowermost tier (Fig. 28–29, 45, 52, 85), which in mature individuals usually



exceed the length of the nearly subequal cells of the second and third tiers (Fig. 1–2, 11–12, 30, 46, 53, 59–60, 64, 67, 73). Other than *T. hebri*, in which a fifth cell could be demonstrated in three of the four rows of outer wall cells (Fig. 11–12), and *T. hydrometrae*, in which five cells were evident in both posterolateral rows (Fig. 30), only the *m* cell-derived row in *T. balazucii*, *T. biformis*, *T. bullatus*, and *T. poissonii* (Fig. 53, 59, 64, 73) included an easily detected and well-defined terminal fifth cell.

Male Individuals of Dioecious Forms

Specimens showing the precise sequence of divisions of the original two cells of the ascospore giving rise to male individuals of *Triceromyces* species (Fig. 47, 58, 65–66, 68, 76, 79–80) were not found. Nevertheless, the course of development probably is the same as in the earliest stages of formation of the monoecious form of *T. biformis* (Fig. 32–34). The lower cell of the ascospore, however, does not divide. Instead it becomes a simple unicellular receptacle, which differentiates the basal foot (Fig. 79). The upper cell of the spore forms three superposed cells with the terminal cell being converted into a simple antheridium (Fig. 79–80).

DISCUSSION

In coining the generic name, *Triceromyces*, Majewski (1981) stressed the three prominent, more or less elongate outgrowths arising from perithecial outer wall cells in the type species, *T. balazucii*. Discovery of *Triceromyces* species having a lesser number of such outgrowths or none has necessitated emendation of the generic description, for these structures clearly have only specific significance in the genus.

Perithecial ontogeny of *Triceromyces* species is like that characteristic of sub-order Laboulbeniineae, family Laboulbeniaceae (Tavares 1985), and Tavares classifies the genus along with 36 others in subtribe Stigmatomycetinae (see Tavares 1985, key to genera, couplets 47–83'). Despite the misplaced emphasis Majewski (1981) put on perithecial outgrowths, *Triceromyces* is retained on the basis of two features found in common and consistently in all of its taxa: (1) the formation of an appendage having a three-celled stipe supporting the antheridiiferous part in monoecious forms and (2) the partition of cell III of the receptacle into an upper part containing nucleated cytoplasm and a lower part lacking cytoplasm in all perithecium-bearing forms. The latter feature is unknown in other Laboulbeniales.

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Fig. 84–88. *Triceromyces poissonii*.—84–85. Monoecious form.—84. Immature individual showing the receptacle with modified cell III, and the three-celled stalk of the primary appendage (*pa*) (RKB 2842).—85. Perithecium at the four wall cell stage of development (RKB 2839). Note centrum (*ce*) surmounted by two of the four tiers of inner wall cells (*p*) between which the trichophoric cell (*tc*) is much compressed.—86–88. Females of dioecious form.—86. Young individual showing immature perithecium with trichogyne (*tr*), two-celled primary appendage (*pa*), and cell III of the receptacle in which the uninucleate mass of cytoplasm has moved into the upper part of the cell (see also Fig. 69) (RKB 2841).—87. Slightly older individual (RKB 2841). The terminal part of the trichogyne is becoming disorganized; the primary appendage is three celled; and the cytoplasm in the upper part of cell III of the receptacle has been delimited from the lower part of the cell by a secondarily formed wall.—88. Receptacle and appendage of a mature individual (RKB 2080). (All figures, bar with Fig. 87 = 10 μ m.)

Species of *Triceromyces* can be viewed as having coevolved along with closely related hosts (Frank 1982; Tavares 1985). Among the families of superfamily Gerroidea (Štys and Kerzhner 1975), Hebridae and Mesoveliidae are perhaps more closely related to one another than they are to Hydrometridae (Polhemus and Chapman 1979a, b, c; Usinger 1956). Insects belonging to these families are carnivorous, like all Gerroidea, and share similar habitats on or near quiet waters with floating or emergent vegetation—ponds, bogs, lakes, small streams—where they seek their prey. Fortuitous transfer of parasites and their subsequent independent development through time (Benjamin 1967) could have led to the appearance of the taxa described here, and surely others yet to be discovered. The genus could have arisen from some *Autophagomyces*-like ancestor. Based on the structure of the antheridium-bearing part of the appendage and to some extent on perithecial characteristics, the six species of *Triceromyces* known at present appear to represent three separate evolutionary lines, one on each of the three host families. Other examples of the coevolution of distinctive laboulbenialean genera on insects belonging to Gerroidea are *Prolixandromyces* on Veliidae (Benjamin 1970, 1981) and *Rhizopodomycetes* on Hebridae (Benjamin 1979) for which a number of species of each genus is known. In a similar vein, species of *Laboulbenia*, a genus of many hundreds of species with hosts in several orders of insects and a few other arthropods (Tavares 1985), are found on Gerroidea and are currently known on members of two closely related families, Macroveliidae and Veliidae (Polhemus and Chapman 1979d; Štys 1976). Despite marked specific differences, species of *Laboulbenia* on mesoveliids and veliids share several distinctive morphological features suggesting their development from a single ancestral *Laboulbenia* (Benjamin 1967, and unpublished).

The question of fertilization and sexuality in the Laboulbeniales has been reviewed by Tavares (1985:83–88). Production of spermatia by antheridial cells has been observed in species representing most genera of the order, and attachment of these presumed male sexual cells to trichogynes has been encountered in several instances. Nevertheless, cytological verification of fertilization in the Laboulbeniales has not been achieved. However, in juvenile thalli the frequent observation of an appendage, which bears spermatia-forming antheridia, juxtaposing a trichogyne, which collapses and disintegrates soon after centrum development begins, suggests the sexual function of spermatia in many if not all of these fungi where they are found. Tavares (1985) has demonstrated diakinesis in the young ascus of the dioecious *Herpomyces periplanetae* Thaxter indicating meiosis; she suggests that one nucleus in the dikaryon probably came from the male thallus.

Of the 132 genera Tavares recognizes in her treatise on Laboulbeniales (Tavares 1985), 114 are demonstrably or presumptively monoecious, both perithecia and antheridia being borne on the same individual. Sexual dimorphism characterizes 12 genera (13 if *Thripomyces* Speg. is dioecious as suspected by Tavares). In these genera, antheridia and perithecia are borne on separate individuals, which often differ in size and thallus complexity. In some genera (e.g., *Dimeromyces* Thaxt., *Dimorphomyces* Thaxt., *Nycteromyces* Thaxt., and *Trenomyces* Chatton & Picard) the receptacle of the male resembles that of the female, differing primarily only in the production of antheridia instead of perithecia. In other genera (e.g., *Amorphomyces* Thaxt., *Apatomyces* Thaxt., *Dioicomyces*, *Picardella* Tavares, *Rhizopodomycetes*, and *Tetrandromyces* Thaxt. [including *Dicrandromyces* Thaxt. and

Triandromyces Thaxt. fide Tavares]) the male consists of a few superposed cells bearing one or only a few antheridia distally. Five genera currently are known to include both monoecious and dioecious species (Tavares 1985). In four of these genera (*Aporomyces* Thaxt., *Cryptandromyces* Thaxt., *Euphoriomyces* Thaxt., and *Nanomyces* Thaxt.) the male of dioecious taxa is reduced in size like that of the taxa named immediately above. In the fifth genus, *Laboulbenia*, species having small, simple males have been described (i.e., *L. vignae* Rossi [1978] and *L. sbordonii* Rossi & Cesari Rossi [1977]); however, both of these species, like *Apatomyces laboulbenioides* Thaxter (1931), occur on Trechinae (Coleoptera: Carabidae) and may belong to *Apatomyces*. In another dioecious *Laboulbenia*, *L. formicarum* Thaxter, male and female individuals are nearly identical except for the absence of perithecia on males and the lack of antheridia on females (Benjamin and Shanor 1950).

The mechanism or mechanisms controlling dioecism in Laboulbeniales are unknown. No species has been cultured, which would be a prerequisite for genetical studies, and the cytological studies by Tavares (1985) on *Herpomyces* Thaxt. offer no clues in this genus. Olive (1958) suggested that differences in growth rates of paired thalli (derived from spore pairs developing adjacent to one another) might be responsible for the differentiation of males and females, the female growing more rapidly than the male. However, as Benjamin (1971) noted, the male of dioecious species actually matures and begins to form spermatia by the time the female has given rise to a young perithecium with a presumably receptive trichogyne. Monoecism, which is predominant in the order, probably is the primitive condition in Laboulbeniales, and dioecism apparently has arisen a number of times as evidenced by its occurrence in several diverse taxa (Tavares 1985).

There is a tendency in species of monoecious genera for one spore of a spore pair to form a normal hermaphrodite and the other spore to be arrested in its development and form only a spermatium-bearing, i.e., male, thallus. A classic example of this was illustrated by Thaxter for *Stigmatomyces sarcophagae* Thaxter (1908:Pl. XLIX, fig. 16–17). Tavares illustrated the same condition in *Hydrophilomyces rhynchophorus* (Thaxter) Thaxter (Tavares 1985:PL. 51f). I have observed the phenomenon on occasion, not only in species of *Stigmatomyces* but in those of other genera as well, including *Autophagomyces* and *Aphanandromyces* Rossi (Benjamin unpubl.). In his attempts to culture *Fanniomyces ceratophorus* (Whisler) Majewski (= *Stigmatomyces ceratophorus* Whisler), Whisler (1968) observed development of "male" thalli in about 12% of his cultures of spores placed on wings of the fly host, *Fannia canicularis*, applied to the surface of an enriched brain-heart infusion agar. Perithecial initials never developed on these thalli in such cultures. The males did, however, closely resemble those occasionally encountered along with normal hermaphrodites on the living fly. Development of a depauperate male individual alongside a normally developed bisexual individual probably is effected by some kind of nutritional imbalance affecting one spore of a spore pair. It is unlikely that the phenomenon has played a role in the evolution of dioecism in the Laboulbeniales.

Herpomyces, the sole genus of suborder Herpomycetinae (Tavares 1981, 1985), includes some 25 species on Blattaria (cockroaches), all dioecious. Tavares (1965) found that normal, spermatium-forming antheridia would develop on aborted females of *H. paranensis* Thaxter. Thus, the potentiality for maleness resides in

the female thallus of this species (and perhaps in those of other species of *Herpomyces*), and male structures apparently are formed only when a female is subjected to stress. Olive (1966) suggested that *Herpomyces* may have arisen from a heterothallic monoecious precursor, and that numerous monoecious species of Laboulbeniales might include both homothallic and heterothallic forms. There is no proof for this credible conjecture, which can only be proved or disproved experimentally.

Dioecism as seen in *Laboulbenia formicarum* (Benjamin and Shanor 1950), in which the male and female are nearly identical and arise from spores of equal size, can be viewed as possibly a primitive condition of recent origin. Tavares (1985:87) suggests that two mutations of hermaphrodites to unisexual thalli could have been operative here, one mutation leading to formation of the male, the other to formation of the female. She further speculates that there may have been a delayed development of the perithecium on the "male" thallus followed by genetic loss of the ability to produce a perithecium in dioecious taxa like *Amorphomyces* and *Herpomyces*. Thus, taxa like those in *Amorphomyces* and *Dioicomycetes* can be viewed as advanced phylogenetically, the male having undergone reduction to a very simple thallus form. Specialization of males of the type found in *Dioicomycetes*, and a few other dioecious taxa, is suggested by the often extreme dimorphism of the pair of ascospores giving rise to males and females, the spore forming the female being large, that forming the male being small (Benjamin 1970:Fig. 3d). Pronounced ascospore dimorphism has been demonstrated in only a few dioecious Laboulbeniales, however, and its interpretation as an indicator of phylogenetic advancement has only limited application, if indeed it should be so considered.

The phenomenon of monoecious-dioecious dimorphism in the species of *Triceromyces* occurring on Mesoveliidae indicates that the development of a simple male alongside a normally developed female is not necessarily the product of long-time evolutionary reduction. Instead, there appears to be a mechanism, probably genetic, operative in these species that results in the production of hermaphrodites together with males and females. Unfortunately, it is not possible at present to know whether or not a regular proportion of these sexual forms arises from spores segregated in a single ascus and whether or not hermaphrodites and unisexuals are cross compatible. It seems unlikely that three species, one occurring in the Western Hemisphere, the other two in the Eastern Hemisphere, could have at the same time evolved monoecious and dioecious forms which are closely associated yet independent of one another in terms of compatibility.

The association of both monoecious and dioecious forms in species of *Triceromyces* provides the first direct evidence that the dioecious condition in the Laboulbeniales could have evolved from a monoecious precursor or vice versa. I prefer the monoecious to dioecious pathway, and the condition observed in the three species studied here can be interpreted as a very early stage in the process. Genetic change and isolation could eventually bring about the elimination of one form or the divergence of both forms leading, on the basis of morphology, to what would be regarded as one or two distinct genera. Failure to recognize the true nature of the dimorphic status of *T. poissonii* led me originally (Benjamin 1970) to assign the monoecious form to *Autophagomyces* and the dioecious form to *Dioicomycetes*. It is possible that other examples of monoecious-dioecious dimorphism exist in the Laboulbeniales. Finding them will require careful inventory

and study of taxa at the time they are removed from their hosts beyond that needed simply for identification or description.

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FOOTNOTE

¹ In the first paragraph of my paper on *Rhizopodomyces* (Benjamin 1979:379), please change long-horned to short-horned in line 11 from the bottom and change short-horned to long-horned in lines 7 and 9 from the bottom.